Effects of Human Activity on Space Use and Movement Patterns of Female Elk

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ABSTRACT It is important to consider how human activity might influence behavior (e.g., space use and movement) in animals because such influences could have consequences for animal distribution or population performance. We documented and compared annual space use and daily movement patterns (i.e., movement distance and tortuosity) of female elk (Cervus elaphus) relative to human activity associated with development of energy resources in Colorado and New Mexico, USA, from 2006 to 2010. We analyzed data on 145 female elk fitted with global positioning system collars. While controlling for elevation, slope, and distance to anthropogenic features and vegetative cover, we found that proximity to the gas field generally was associated with smaller home ranges, more complex movement paths (i.e., greater tortuosity) and longer distance moved over a 3-hr period (during most seasons). Comparing elk inside of the gas field to those outside of the gas field revealed differences in space use and movement patterns at varying levels of human activity. These differences likely reflected behavior by which elk in industrial areas attempted to minimize contact with sources of human activity; whereas, elk using both industrial and nonindustrial areas exhibited behavior that could be considered escape strategies (i.e., familiarity and use of large spatial extents, increased movement distance, and linear movement paths) in response to seemingly unpredictable levels of human activity due to their use of multiple areas. Understanding such behavioral responses informs efforts to minimize effects of human activity on animal populations. © 2011 The Wildlife Society.

KEY WORDS Cervus elaphus, Colorado, disturbance, elk, energy development, home range, human activity, movement, tortuosity.

Humans continually alter the face of the landscape. Human activity tends to reduce or fragment important wildlife habitat, potentially leading to large-scale biological changes such as modified hydrologic cycles or altered vegetation communities (Saunders et al. 1991). Such change can influence persistence of animal populations by affecting patterns of occupancy, distribution, dispersal, or colonization (Russell et al. 2003). Movement and space-use behavior are fundamental processes structuring these patterns. In places where human activity is widespread or increasing, understanding how human activity interacts with other landscape features to affect animal movement and space-use behavior is necessary for identifying impacts and developing management strategies.

Elk (Cervus elaphus) are high-priority management species throughout the western United States. Here, energy development (e.g., coal-bed methane gas) is of broad conservation interest because its prominence has increased in recent decades along with concern about its potential impact on elk and other ungulate populations (Sawyer et al. 2006, 2009a).

Features of natural gas development include networks of roads (and other rights-of-way) and well pads, as well as an increase in human activity throughout the development area; all of which may hinder ungulate movement (Sawyer et al. 2009b) either directly or indirectly. A broad-range of human activity affects space use and movement of ungulates. For example, hyrdoelectric dams (Andersen 1991), military maneuvers (Andersen et al. 1996, Stephenson et al. 1996), logging (Edge et al. 1985), ranching operations (Hood and Inglis 1974), simulated mining (Kuck et al. 1985), installation of oil wells (Van Dyke and Klein 1996), and other industrial development activities (Bradshaw et al. 1997, Dyer et al. 2001) are known to influence movement behavior.

There is still much to be learned about the effects of various human activities on animal behavior, demography, fitness, and resource use. For example, information on how elk respond to landscape-level development of energy resources is scarce in published literature. We analyzed data within a treatment–control framework in which human activity associated with industrial development was considered the treatment. Assignment to groups depended on whether individual elk occupied a producing natural gas field (i.e., industrial) versus areas outside of the gas field (i.e.,
We also analyzed a third group that included elk that moved between the gas field and adjacent areas, thus occupying both industrial and nonindustrial areas (i.e., transition). A primary goal of this work was to investigate whether the responses differed among treatment groups while accounting for covariates that simultaneously influenced the responses. Our objectives were to 1) compare space-use patterns (i.e., annual home range size) among treatment groups, and 2) document and compare daily movement distance and tortuosity across seasons relative to treatment group. Based on previous analyses of this population of elk (Dzialak et al. 2011, Harju et al. 2011; Webb et al. 2011), we knew a priori that behavior primarily was affected by human activity, resulting in modified space use and resource selection within areas of human activity, but mitigated by landscape covariates. Therefore, we make the following predictions: 1) elk movement will be constrained within previously established ranges where size of the home range is dependent on level of human activity; 2) individuals will adjust movement behavior to human activity that partially will be dependent on landscape features; and 3) individual heterogeneity and functional responses (Dzialak et al. 2011, Harju et al. 2011) will make predicting group-specific movement behavior difficult, but still will provide a measure of the effects of human activity on movement and space use.

**STUDY AREA**

The study area was located in the northern portion of the Raton Basin in Costilla, Las Animas, and Huerfano counties of south-central Colorado, and Colfax and Taos counties in northern New Mexico (USA, Fig. 1). Land ownership was predominately private, which comprised approximately 89% of the area (Vitt 2007). Ranching, hunting, energy development, and some second-home development were the predominant land use practices. The core of the study area (i.e., the gas field) encompassed historic and ongoing coal-bed natural gas development. As of 2009, there were 2,421 well pads (1.77 well pads/km²) and 2,933 wells (2.14 wells/km²) in the Raton Basin. Based on coal-bed natural gas development, we divided the study area into 2 regions: a region inside of the gas field (1,370 km²) and a region outside of the gas field (2,712 km²; Fig. 2). We placed a 2-km buffer around all wells and refer to the region within the buffer area as “inside of the gas field.” We refer to areas adjacent to, but outside of this buffer, as “outside of the gas field.” In the section titled *Analysis* below, we specify how elk were assigned to groups (industrial, nonindustrial, transition) based on their occurrence in these 2 study area regions (inside vs. outside of the gas field). Human modifications of the landscape inside of the gas field included: well pads and associated structures, communities, residences, buildings, industries, ranching activities, roads, railroads, and pipelines. Human modifications outside of the gas field included the aforementioned disturbances except for well pads and associated structures. Therefore, our analyses quantify whether any differences exist in space use and movement of female elk relative to human modifications associated with energy development, which was present in one area but not the other, similar to previous analyses (Dzialak et al. 2011, Harju et al. 2011). Although roads were present in both areas, road density was 2.2 times greater inside of the gas field (2.4 km/km²) compared to outside (1.1 km/km²). Average size (ha) of disturbances were 1.5 (±0.15 SE) for ranching, 3.2 (±0.73) for industrial development, 17.2 (±13.63) for community, 0.3 (±0.02) for residences, and 0.5 (±0.01) for well pads. The ratio of habitat unmodified to that modified by humans was 32:1 inside the gas field and 45:1 outside the gas field. Landscape covariates (i.e., slope, forest cover, convexity, and elevation) were similar within and outside of the gas field except for distance to edge (junction between open fields and forest patches), which suggests that vegetative communities were more contiguous outside of the gas field (Harju et al. 2011).

Topography ranged from rolling ridges and valleys to steep alpine slopes and cliffs (Vitt 2007) with elevation ranging from 1,800 m to 4,300 m. Dominant plant species included ponderosa pine (*Pinus ponderosa*), one-seed juniper (*Juniperus monosperma*), two-needle pinyon (*Pinus edulis*), Gambel oak (*Quercus gambelii*), antelope bitterbrush (*Purshia tridentata*), skunkbush sumac (*Rhus trilobata*), and willow (*Salix spp.*). Mean annual precipitation ranged from 15 cm at lower elevations to 51 cm at higher elevations (Vitt 2007). We...
obtained site-specific temperature data from 7 weather stations located across our study area at elevations ranging from 1,983 m to 2,841 m. At the highest elevation weather station, minimum and maximum January and July temperatures were −26.3°, 12.4°, 3.2°, and 26.4° C, respectively. Minimum and maximum January and July temperatures were −25.2°, 20.9°, 7.1°, and 33.8° C, respectively, at the lowest elevation weather station.

METHODS

Capture and Handling
We captured yearling (1.5 yr) and adult (≥2.5 yr) female elk, using a helicopter and either a dart-gun or net-gun, annually during February and March 2006–2009. Darted elk were anesthetized using either carfentanil or thiafentanil (A-3080), further restrained with hobbles, and fitted with blindfolds. Naltrexone was used as an antagonist to both carfentanil and thiafentanil. Animals captured using the net-gun were manually restrained with hobbles and fitted with blindfolds to reduce stress. We estimated age of elk using tooth eruption, replacement, and wear techniques (Quimby and Gaab 1957). Elk were fitted with a global positioning system (GPS) collar (TGW-3590; Telonics, Inc., Mesa, AZ) and released at site of capture. We fitted 165 elk with GPS collars; 25, 40, 50, and 50 during 2006, 2007, 2008, and 2009, respectively. After excluding fatalities and several collar malfunctions, data for 145 GPS-collared elk were available for analysis. Age of females at time of capture ranged from 1 yr to 12 yr (x = 5.6 ± 0.2 SE; median = 5). Animal capture and handling protocols were followed (Gannon et al. 2007) and approved by the Colorado Division of Wildlife (Permit no. 06TR1083, 07TR1083, 08TR1083, and 09TR1083A001).

Movement
Global positioning system collars were configured to record location data every 3 hr (i.e., max. of 8 relocations/day) for approximately 1 yr. We downloaded data from collars remotely every 2–4 weeks or after retrieval of the released collar. After download, data were brought into a geographic information system to calculate step-length (hereafter, movement distance) and tortuosity. Movement distance (L) was calculated as the straight-line distance between successive locations. Tortuosity is a measure used to estimate path complexity, and is calculated by dividing movement distance (L) by net displacement (R; Whittington et al. 2004). Net displacement is the distance between the very first location and the current location in the dataset for each individual elk. Similar to Whittington et al. (2004) and Turchin (1998), we modeled tortuosity as L/R² because R² typically increases linearly with path length (L). Before analysis, we log-transformed tortuosity (L/R²) to correct heteroscedasticity and a right-skewed distribution, and to help meet normality assumptions (Whittington et al. 2004).

Tortuosity has been used to describe path complexity or linearity, and intensity of use of an area. Tortuosity is a relative measure of path complexity or linearity and intensity of use of an area because it is based on the ratio L/R². Values can range from zero to ∞, where values nearer to zero represent more linear movements, simpler movement trajectories, and reduced use of an area, while increasing values represent more tortuous or complex movements, and increased use of an area.

We analyzed movement metrics at the scale of the daily cycle (within-season). Within-day movement distance and tortuosity were estimated across 8 3-hr time blocks. To increase precision of movement parameters for a 3-hr time block, we only considered and analyzed consecutive 3-hr locations. If a data point was missing, creating a 6-hr time block (for example), we excluded the movement estimates and used the next set of consecutive locations that resulted in 3-hr separating locations. We defined 4 seasons based on biological and environmental variables. Calving and lactation season (hereafter, calving) was defined as 15 May to 15 August; rut and early hunting season (hereafter, rut) from 16 August to 31 October; winter and late hunting season (hereafter, winter) from 1 November to 15 March; and late gestation and spring green-up season (hereafter, gestation) from 16 March to 14 May.

Space Use
As a measure of the annual extent of space use, we calculated annual size of 95% home ranges using adaptive-kernel methods (Worton 1989) in Home Range Tools (Rodgers et al. 2005) for ArcGIS® 9.3 software. Annual home range was calculated from March through February of the following year. We used unit-variance standardizations and
the biased cross-validation smoothing parameter when calculating volume-probability polygons.

**Development and Calculation of Covariates**

We calculated 4 covariates depicting anthropogenic and landscape features that influence spatial dynamics of elk in this population (Dzialak et al. 2011a, b; Harju et al. 2011; Webb et al. 2011a). We delineated the following anthropogenic features: well pads and ancillary facilities, residences, buildings, industries, roads, railroads, pipelines, and ranching activities. Features were interpreted, digitized, and attributed based on annual aerial photography (2005–2009). We used heads-up digitizing of all visible surface features within our study area and performed all spatial analyses using ArcGIS® 9.3 software. All anthropogenic features were merged into a single feature layer depicting landscape-level human activity. We calculated the distance to the nearest anthropogenic feature from each location using a join feature based on spatial location in ArcGIS® 9.3.

We calculated elevation (m) and slope (°) using a 10-m digital elevation model (DEM). Slope was calculated from the DEM using Surface Tools within Spatial Analyst of ArcGIS® 9.3. Based on DEM, elk used elevations ranging from 1,854 m to 4,152 m.

Last, we calculated distance to nearest vegetative cover patch, which included riparian, closed-canopy forest, open-canopy forest, and oak-dominated shrubland. We developed the vegetation cover-type map using high-resolution (0.3-m) true-color and color-infrared (CIR) aerial photography and Feature Analyst® 4.2 (FA) for ArcGIS® (Visual Learning Systems, Inc. 2008). We conducted a supervised classification using delineated polygons of known vegetation type for use with object-based feature-extraction algorithms. The true-color and CIR bands were combined using FA, which resulted in 4 spectral bands (i.e., red, green, blue, and near-infrared). We also specified the green spectral band to be used to develop a texture band. We used DEM to develop an elevation band, which finally resulted in 6 bands (i.e., 4 spectral bands, 1 texture band, and 1 elevation band). Last, we varied our resolution or pixel classifier pattern and size combinations based on vegetation type. Prior to running classifiers, we resampled vegetation cover types that occurred over extensive areas (i.e., closed-canopy forest, open-canopy forest, oak-dominated shrubland, alpine, and grassland) to 3-m resolution and vegetation cover types that were more restricted or linear (i.e., riparian) to 1.5-m resolution. We used the Manhattan classifier pattern and a width of 7 pixels to classify extensive vegetation types. For more restricted vegetation types, we used the Bull’s Eye 2 classifier and a width of 15 pixels. We reclassified our 6 vegetation classes into either vegetative cover or non-vegetative cover. We considered all vegetation classes as vegetative cover except alpine and grassland vegetation types. We converted our vector vegetation map, which consisted of 2 classes (vegetative cover or non-vegetative cover), to a raster image and calculated the Euclidean distance from each cell to the nearest cell containing cover. Last, we extracted raster values from our Euclidean-distance-developed image to each elk location using Spatial Analyst for ArcGIS® 9.3.

**Analysis**

A primary goal of this work was to investigate whether the responses differed among groups (industrial, nonindustrial, and transition) while accounting for the potentially confounding effects of other landscape features that are known to influence space use and movement in ungulates. For analysis, we partitioned each elk among 3 treatment groups (Table 1) depending on their use of the landscape relative to the natural gas field (Fig. 2). Elk were partitioned as follows: 1) industrial group—≥90% of annual locations occurred inside the gas field; 2) nonindustrial group—≥90% of annual locations occurred outside the gas field; and 3) transition group—any elk not meeting aforementioned classifications (i.e., elk used both industrial and non-industrial areas). Hereafter, we refer to groups of elk as industrial, nonindustrial, and transition.

Before analysis, we screened movement data for abnormal movement distances. We removed 98 locations due to abnormalities such as movement associated with transport of elk after harvest and abnormal movements such as immediately after capture and on the day of collar release. Observations >3 hr apart also were excluded. We used a square-root transformation to normalize movement distance and to satisfy normality assumptions for statistical tests.

We conducted a multivariate analysis of variance (MANOVA; PROC GLM; SAS 9.2®, Cary, NC) with random effects on our 2 response variables (i.e., movement distance and tortuosity) to determine whether treatment group, elevation, slope, distance to anthropogenic features and cover, and season × hour interaction influenced the response variables simultaneously (O’Rourke et al. 2005: 279–297). Treatment group was a classification variable with 3 levels: 1) industrial (elk using inside of the gas field), 2) nonindustrial (elk using outside of the gas field), and 3) transition (elk using both industrial and nonindustrial areas). Elevation, slope, and distance to nearest anthropogenic

| Table 1. Season-specific sample sizes of female elk (Cervus elaphus) and total relocations based on use of areas inside (i.e., industrial), outside (i.e., nonindustrial), and both inside and outside (i.e., transition) of the gas field located in south-central Colorado, USA during 2006–2010. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Season          | Inside gas field | Outside gas field | Inside and outside | Total          |                  |
|                 | Elk Relocations | Elk Relocations  | Elk Relocations  | Elk Relocations  |                  |
| Calving         | 64              | 47,054           | 26              | 16,491          | 52              | 35,720          | 142              | 99,265          |
| Gestation       | 66              | 31,674           | 27              | 11,910          | 52              | 24,000          | 145              | 67,584          |
| Rut             | 60              | 33,109           | 24              | 11,589          | 52              | 27,451          | 136              | 72,149          |
| Winter          | 64              | 55,153           | 25              | 19,546          | 52              | 47,456          | 141              | 122,155         |
| Total           | 166,990         | 59,536           |                  | 134,627         |                  |                  | 361,153          |
feature and cover patch were continuous variables. We also considered a season × hour interaction because of inherent differences in behavior of ungulates over daily and seasonal cycles (Craighed et al. 1973, Green and Bear 1990, Ager et al. 2003, Kie et al. 2005). To account for pseudo-replication in measurements taken on the same elk within the same year, we specified elk identification nested within year as a random effect (i.e., random intercept). To assess how important each explanatory variable was on both response variables simultaneously, we used a multivariate measure of association called Wilk’s lambda (O’Rourke et al. 2005:279–297). Values of Wilk’s lambda range from 0 to 1, but are interpreted differently than measures of association (e.g., $r^2$ or $R^2$). Values near 0 indicate a relatively strong relationship, whereas values closer to 1 indicate a relatively weak relationship. We also requested and examined the univariate tests for each response variable to determine how each response variable contributed to the overall MANOVA. Last, we requested that the solution effects (i.e., parameter estimates) for each explanatory variable be printed so we could determine the relationship (i.e., positive or negative) between the explanatory variables and each response variable.

To evaluate differences in extent of space use (i.e., annual home range size) among the 3 treatment groups, we used a one-way analysis of variance (PROC GLM; SAS 9.2®). All means are reported ± standard error. For visual purposes, we report and plot actual movement distances and tortuosity, not the transformed values used for statistical tests.

RESULTS

Collars ($n = 145$) collected 379,454 GPS locations over 4 yr. However, we only used GPS locations separated by 3 hr resulting in 361,153 locations for statistical analysis (Table 1). Average location error of 471 fixes from test collars was 12.8 m (±1.3 SE).

Multivariate analysis of variance revealed that both movement distance and tortuosity simultaneously were influenced by all 6 explanatory variables. However, due to the large sample, some independent variables were only weakly correlated with movement. Despite weak correlations, we report all results, interpret the direction of the sign of parameter estimates for biological meaning, and discuss parameter estimates relative to one another rather than in terms of their influence on the response. The season × hour interaction had the strongest association with the responses (movement distance and tortuosity; Wilk’s lambda = 0.772; $F_{6,2721,390} = 1.607; P < 0.001$). Treatment group (Wilk’s lambda = 0.839; $F_{4,721,390} = 16.538; P < 0.001$) and elevation (Wilk’s lambda = 0.86; $F_{2,360,695} = 29.390; P < 0.001$) also had a relatively strong association with the responses. Distance to anthropogenic features (Wilk’s lambda = 0.945; $F_{2,360,695} = 10.575; P < 0.001$), slope (Wilk’s lambda = 0.988; $F_{2,360,695} = 2.100; P < 0.001$), and distance to vegetative cover (Wilk’s lambda = 0.999; $F_{2,360,695} = 19.6; P < 0.001$) were weakly associated with the responses.

Individual univariate tests for movement distance ($F_{255,360,696} = 423; P < 0.001$) and tortuosity ($F_{255,360,696} = 1,064; P < 0.001$) also were significant; however, a greater proportion of the variability in tortuosity ($R^2 = 0.49$) was explained by the model in comparison to movement distance ($R^2 = 0.23$). Movement distance and tortuosity were influenced negatively by elevation ($\beta_{\text{dist}} = -0.002 ± 0.016$ SE; $\beta_{\text{tort}} = -0.01 ± 0.001$ SE; $\beta_{\text{dist}} = -0.105 ± 0.002$ SE), distance to anthropogenic features ($\beta_{\text{dist}} = -0.001 ± 0.001$ SE; $\beta_{\text{tort}} = -0.001 ± 0.001$ SE; $\beta_{\text{dist}} = -0.001 ± 0.001$ SE), and distance to vegetative cover ($\beta_{\text{dist}} = -0.001 ± 0.001$ SE; $\beta_{\text{tort}} = -0.001 ± 0.001$ SE; $\beta_{\text{dist}} = -0.001 ± 0.001$ SE); as each of these 4 explanatory variables increased, movement distance and tortuosity decreased. Using the nonindustrial group of elk as a baseline reference, we found elk in the industrial group moved more tortuously (0.381 ± 0.106 SE) than the nonindustrial group, whereas the transition group moved more linearly (−0.189 ± 0.103 SE). Compared to the nonindustrial group, elk in industrial (4.762 ± 0.421 SE) and transition (7.442 ± 0.411 SE) groups generally moved longer distances over a 3-hr period. The finding that elk in the industrial group generally moved longer distances may have been driven by increased movement during reproductive seasons (i.e., rut and calving; Fig. 3A,D), which masked reduced movement during nonreproductive seasons (Fig. 3B,C).

Based on plots of untransformed movement distance and tortuosity, all 3 groups of elk exhibited crepuscular patterns of movement, although differences did exist within and across seasons and hours (Figs. 3 and 4). Movement (Fig. 3) and tortuosity (Fig. 4) were greatest from 0600 hours to 0900 hours and 1800 hours to 2100 hours. Several general patterns also were revealed irrespective of more fine-scale differences in movement across hours. One general pattern of interest was that movement distance was dampened across all hours during winter (Fig. 3B) compared to other seasons (Fig. 3A,C,D). Also of interest, elk in the transition group moved more linearly (i.e., lower tortuosity) during rut (Fig. 4A) compared to the other 2 groups of elk. Lastly, during calving, elk in the industrial group moved more tortuously (i.e., more complex movement paths) than elk in the other 2 groups (Fig. 4D).

Home range size is a common metric used to estimate the extent of space use in animals. We estimated annual size of home ranges to elucidate the effects of human activity at longer temporal scales. Average annual home range size of all elk was 26,477 ha (±2,018 SE). Elk in the industrial group maintained smaller home ranges (14,777 ha ± 1,065 SE) compared to elk in the nonindustrial group (29,036 ha ± 2,462 SE) and elk in the transition group (39,870 ha ± 4,546 SE; $F_{2,139} = 20.2, P < 0.001$).

DISCUSSION

Female elk generally exhibited different patterns of movement and space use depending on their location relative to an operating natural gas field and associated human activity. In this population of elk, human activity associated with energy development (i.e., industrial group) was one of the most influential variables (relative to other variables analyzed) on movement, after die and seasonal cycles (i.e.,

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However, the complexities that arise from variable levels of human activity and risk make predicting behavior difficult for several reasons. First, human activity (similar to predation risk) can impose selection pressures on animals that make them unable or unwilling to respond to features of their landscape in ways that they normally would have (Winnie et al. 2006). Second, in this human-modified landscape, there appears to be a pattern in which variation among individuals is amplified, yet within-individual variation is constrained relative to elk in less-modified areas (Dzialak et al. 2011a; Harju et al.)

Figure 3. Mean 3-hr movement distance (m) of female elk (Cervus elaphus) inside (solid black line) and outside (gray line with long dashes) of the gas field in the northern portion of the Raton Basin located in Costilla, Las Animas, and Huerfano counties of south-central Colorado, and Colfax and Taos counties in northern New Mexico (USA) during rut (A = 16 Aug–31 Oct), winter (B = 1 Nov–15 Mar), gestation (C = 16 Mar–14 May), and calving (D = 15 May–15 Aug), 2006–2010. Elk using both areas are represented by gray lines with short dashes. Error bars represent ±1 standard error.

Figure 4. Mean 3-hr estimate of tortuosity for female elk (Cervus elaphus) inside (solid black line) and outside (gray line with long dashes) of the gas field in the northern portion of the Raton Basin located in Costilla, Las Animas, and Huerfano counties of south-central Colorado, and Colfax and Taos counties in northern New Mexico (USA) during rut (A = 16 Aug–31 Oct), winter (B = 1 Nov–15 Mar), gestation (C = 16 Mar–14 May), and calving (D = 15 May–15 Aug), 2006–2010. Elk using both areas are represented by gray lines with short dashes. Error bars represent ±1 standard error.
It is thought that these observations reflect situation-specific responses by elk to widespread and dynamic human activity. Both of the aforementioned observations can make specific predictions on animal movement difficult, largely due to individual heterogeneity that likely is present within groups and the fact that female elk show strong site fidelity (Webb et al. 2011a) even in the presence of rapidly changing landscapes (Dzialak et al. 2011a). Although a statistical link between level of human activity and movement behavior was observed, strong associations between movement parameters and covariates were less apparent, albeit present. Therefore, we offer several hypotheses for the associations and what they mean in terms of elk management within human-modified landscapes.

Elk occupying industrial areas reduced their space use, moved farther between successive locations, and showed increased complexity, or tortuosity, of movement (particularly during calving season) relative to elk using nonindustrial areas. In ungulates, formation of home ranges typically extends over several years (Nelson and Mech 1984, Webb et al. 2007); thus, elk have had time to form home ranges and adjust size in relation to human activity and disturbance that minimizes direct and indirect effects on the animal (Webb et al. 2011a). Reducing extent of space use has been proposed as a strategy to minimize contact with anthropogenic features or human activity (Webb et al. 2011a); elk exhibited similar behaviors in response to logging activity (Edge et al. 1985). The finding of a general influence of human activity on space use reflects longer term processes by which level of human activity affects space-use behavior. A component of such longer term processes includes acute, or shorter term, responses such as day-to-day avoidance of human activity.

Webb et al. (2009) proposed that tortuosity of individual animal movement paths was related to extent of space use. We examined whether tortuosity of individual elk movement paths was related to extent of space use in a post hoc analysis to further explain the link between movement and home range size. We observed the same negative relationship between tortuosity and home range size (−7,831 ± 681 SE); as tortuosity increased home range size decreased ($F_{1,138} = 132.1; P < 0.001; r^2 = 0.49$), which indicates that elk used smaller areas more intensively. The finding that elk within industrial areas use smaller areas more intensively corroborates the aforementioned movement strategy to avoid coming in contact with features perceived to be risky, such as anthropogenic features where human activity occurs.

Also of interest, as it relates to treatment group, are the space-use and movement patterns of transition elk that used both industrial and nonindustrial areas. Compared to industrial and nonindustrial groups, elk in the transition group traveled longer distances, had the most linear movement paths, and largest home range size (1.4 and 2.7 times larger than nonindustrial and industrial groups, respectively). These types of movement behavior may stem from the variable circumstances that the transition group encountered by using both industrial and nonindustrial areas. Previous research showed that elk were spatially aware of their surroundings and changed their resource use patterns relative to varying levels of human activity (Dzialak et al. 2011a). This finding provides support that elk using transition areas were aware of the variable nature of human activity. Similarly, elk were effective at assessing risk from human hunters, which allowed them to respond accordingly (Proffitt et al. 2009). Thus, elk are able to adopt movement behavior that provides the most appropriate escape strategy when encountering differing levels of human activity, and that may appear unpredictable due to movement into and out of areas with intense human activity. When encountering unpredictable human activity, potential escape strategies include using and becoming familiar with larger areas, moving longer distances, and moving more linearly, all of which were exhibited by elk using transition areas.

Examining movement across seasons and treatment groups revealed patterns as they relate to timing of reproduction. We found, on average, elk within the industrial area moved longer distances than elk in the nonindustrial area. However, examination of season × hour plots (Fig. 3) revealed finer trends in movement distance. The general observation of longer movement distance (5–10% greater) among elk that occupied the industrial area was driven largely by increased movement during 2 seasons: the rut and calving season. However, during winter and gestation, elk in industrial areas moved less than elk in nonindustrial areas. Most mammals are sensitive to human activity during reproduction (Phillips and Alldredge 2000, Cameron et al. 2005). Elk using industrial areas may have moved more to maintain a safe distance from humans and areas of human activity. Because measures of reproductive performance (e.g., lifetime reproductive success, conception rate) are important to fitness, elk likely are more sensitive to human activity during reproduction periods, causing elk to move longer distances to escape the perceived risks. On the other hand, during nonreproductive seasons, elk may prefer to minimize movements to increase probability of survival (Webb et al. 2011a), avoid contact with human activity, or maximize energy gain for future reproductive events.

Location of elk relative to the gas field influenced movement distance and tortuosity but did not appear to affect daily and seasonal rhythms (e.g., crepuscular movement patterns). Most studies have found the same general pattern in elk movement and activity rhythms; elk tend to move more and be most active near sunrise and sunset (Craighead et al. 1973, Green and Bear 1990, Ager et al. 2003, Kie et al. 2005) with few factors significantly altering these patterns. Despite consistent daily movement rhythms, there were dampened peaks in crepuscular movement distance during winter. Movement may have been less for all 3 groups during winter to conserve energy (Moen 1976), which typically is limiting in seasonal environments (Hobbs et al. 1982) such as on our study area. If foraging is the primary daily activity of elk (Green and Bear 1990), requiring movement within and among foraging patches, then movement confined to smaller areas can conserve energy and reduce energy and nutrition requirements (Moen 1976, Gates and Hudson 1979). Movement during winter also has been found to be reduced because forage is of lower quality during this time, requiring longer passage rates
and increased rumination time (Green and Bear 1990). Therefore, in response to lower forage quality, longer passage rates and increased rumination, elk do not move as much to forage.

Females using the industrial area responded to perceived risks related to human activity (Frid and Dill 2002). Females used smaller areas more intensively (i.e., increased tortuosity), potentially as a strategy for protecting offspring. The observation that movement distance was not substantially reduced during calving season, although dampened during the evening, further supports the notion that elk intensely patrolled the area near to where the offspring is hidden. Intensively using a smaller area reduces the likelihood that the female, and the calf when mobile, will encounter humans or anthropogenic features. These movement and space-use patterns may lead to greater fitness if these behaviors lead to greater offspring survival. Females in the other 2 groups may have been able to move more linearly, covering greater areas without the expectation of coming into contact with risks associated with human activity, which was less as the female moved away from the gas field.

Vegetative cover and topographical features influenced movement of female elk and likely interacted with human activity in ways that minimized disturbance to elk. Movement distance decreased as elk used areas farther away from vegetative cover. Therefore, elk may minimize movement when farther away from cover to reduce the probability of being detected. However, while near vegetative cover, elk may feel more secure to move longer distances in the presence of escape cover even when human activity is nearby. This finding corroborates previous findings that vegetative cover mitigates some of the impacts human activity and risk have on animal behavior (Edge et al. 1985, Kuck et al. 1985, Unsworth et al. 1998, Anderson et al. 2005, Rumble et al. 2005). Geist (2002) also recognized that elk might be able to increase their tolerance of human activity in heavily forested areas. Survival and reproduction are known to be enhanced by using areas with greater vegetative cover and by minimizing contacts with humans and anthropogenic features (Garshelis 2000), which is supported by other work on this same population of elk (Dzialak et al. 2011a, Webb et al. 2011b). In a companion study, we found that probability of a female surviving increased as the proportion of vegetative cover increased within areas used by elk in each of the 3 treatment groups (Webb et al. 2011a).

Herein, we have provided evidence that level of human activity, rather than just the type of human activity, has important influences on behavior in elk (i.e., space use and movement). Behavioral responses may occur regardless of the type of human activity. Level of human activity from all sources may be the driving force that influences behavior. We can infer from these data that human activity associated with energy development is an important factor that influences female elk movement. Elk exposed to high levels of human activity may be forced to alter their behavioral strategies to avoid contact with humans or anthropogenic features; factors that have been found to influence probability of mortality (Dzialak et al. 2011a, Webb et al. 2011b).

**MANAGEMENT IMPLICATIONS**

Actions to limit human activity provide a means to minimize behavioral changes by wildlife. Concentrating activities within areas less preferred by elk provides an additional management strategy. Vegetative cover is important for elk; thus, large blocks of vegetative cover within proximity of one another alleviates some of the impacts human activity has on elk behavior. In addition to vegetative cover, topography also will be important to consider as factors to minimize disturbance to elk. Vegetative cover and topography (e.g., elevation and slope) can reduce the line-of-sight of anthropogenic features by elk (Edge and Marcum 1991). Therefore, placing roads, well pads, or any other anthropogenic feature out of the line-of-sight to elk will help mitigate the influence of human activity on elk behavior at these sites. If undisturbed, elk are likely to remain inactive during midday while in dense vegetative cover (Rumble et al. 2005); a general pattern revealed by elk in nonindustrial areas.

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