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SPACE USE OF FEMALE ELK (*CERVUS CANADENSIS NELSONI*) IN THE BLACK HILLS, SOUTH DAKOTA

Tess M. Gingery^{1,3}, Chadwick P. Lehman¹, and Joshua J. Millspaugh²

ABSTRACT.—Following recent elk (*Cervus canadensis nelsoni*) population declines in South Dakota, we evaluated space use of elk in response to biotic and abiotic covariates at a regional scale. We built Brownian bridge movement models to examine summer (parturition date to 31 October) and winter (1 November to following year's parturition date) seasonal movements of radio-collared female elk from 2011 to 2013 at 99% home range and 50% core area contour levels. Our primary objective was to evaluate seasonal movements of female elk in response to drought, vegetation resources, and road density. Higher road densities and increased amounts of open-canopied vegetation were correlated with an increase in core area size. Elk inhabiting open-canopied areas may increase their movements in an attempt to find cover and avoid disturbance factors associated with roads. The high levels of human visitor activity in the Black Hills and accompanying disturbance of wildlife highlight the importance of management strategies that consider elk security cover, or lack of cover in open-canopied areas, when devising road management strategies.

RESUMEN.—Evaluamos el uso espacial del alce (*Cervus canadensis nelsoni*) en respuesta a covariables bióticas y abióticas a escala regional, luego del reciente declive de la población en Dakota del Sur. Construimos Modelos de Movimiento de Puente Browniano para examinar el desplazamiento estacional, en verano (fecha de parto–31 de octubre) y en invierno (1ero de noviembre–siguiente año después del parto) del 2011 al 2013, de alces hembra con radio-collares en 99% del rango local y en 50% del área central. Nuestro objetivo principal fue evaluar los movimientos estacionales de alces hembra en respuesta a un período de sequía, a recursos de vegetación y a la densidad de caminos. Una mayor densidad de caminos y un aumento en la vegetación del dosel abierto se correlacionaron con un incremento en el tamaño del área central. Los alces que habitan en áreas de dosel abierto pueden desplazarse más al buscar refugio y evitar factores de perturbación asociados a las carreteras. Los niveles altos de actividad humana y el potencial de su perturbación en Black Hills, destacan la importancia del manejo de refugios seguros para los alces, o a la falta de refugios en las zonas abiertas, al gestionar el manejo de los caminos.

The way a species uses space can indicate which high-use resources are needed for its proper conservation at a region-specific level (Millspaugh 1995). Assessments of home range size have been used to observe behavioral responses and adaptability of elk to human disturbances (Harris et al. 1990, Millspaugh 1999, Benkobi et al. 2005), and can act as a proxy for evaluating resource conditions such as forage quality and quantity (Kapfer et al. 2010, Mitchell and Powell 2012, Goldingay 2015). Estimation of home range size can also aid in the evaluation of population dynamics, foraging behaviors, and resource distribution (Harris et al. 1990). Previous models estimating home range size have been scrutinized for creating biased estimates of space use and for misidentifying areas of high use (Millspaugh 1999, Mitchell and Powell 2004, Benhamou and Cornelis 2010, Goldingay 2015). We utilized Brownian bridge movement models

(BBMMs), which are more efficient than other models when small time intervals between successive locations are available, to provide a stochastic model through time and space (Horne et al. 2007).

Documentation of core areas, areas of intensive use that likely include optimal shelter and foraging sites, is a key aspect of home range studies (Goldingay 2015). Within a species, large core areas can indicate depressed local resources, inflated energy expenditure, and the necessity of enlarging conservation areas (Benkobi et al. 2005, Goldingay 2015). Core areas have been observed to expand in response to roads, vegetation attributes, and drought (Rumble and Gamo 2011, Montgomery et al. 2012, Middleton et al. 2013). However, space use that is affected by factors such as these can be influenced by interactions between landscape characteristics (Proffitt et al. 2013). For

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example, a combination of both rugged terrain and vegetative security cover can be more effective than vegetative cover alone in encouraging wildlife to use space near roaded areas (Edge and Marcum 1991, Millspaugh et al. 2000, Rowland et al. 2000, Montgomery et al. 2012). Further, the spatial distribution of these resources can influence space use as wildlife attempt to minimize the distance they traverse and maximize access to resources such as food and shelter (Mitchell and Powell 2004, Goldingay 2015).

Elk (*Cervus canadensis nelsoni*) make space use decisions in climates, in vegetative communities, and at levels of human disturbance that are all highly variable (Rumble et al. 2005, Stubblefield et al. 2006, Rumble and Gamo 2011, Montgomery et al. 2013). Custer State Park (CSP) in the southern Black Hills (South Dakota, USA) has 1.6 million annual visitors, resulting in high levels of disturbance for a nonmigratory elk population that has been declining since 2006 (South Dakota Department of Game, Fish and Parks 2015, Lehman 2015). The changes in movement patterns and space use that follow anthropogenic habitat modification can alter biodiversity and individual fitness (Seebacher and Post 2015). Previous analyses of space use in CSP elk were completed when elk populations were higher than at any time in the past century or were limited to examination of summer ranges (Benkobi et al. 2005, Montgomery et al. 2013, Ranglack et al. 2016). Declining elk populations and increasing numbers of human visitors to CSP during recent years justify analyzing current conditions to aid in making effective resource management decisions.

Our objective was to quantify BBMM 99% home range and 50% core area contours, and to model core area size in response to road density, vegetation attributes, and drought. We hypothesized (1) that high road densities would be associated with increased core area size (Rumble et al. 2005, Montgomery et al. 2013), (2) that open-canopied vegetative resources would be associated with larger core area size (Morellet et al. 2013), and (3) that core area size would be larger during a year of drought (2012) (Börger et al. 2006).

Our study area was located in the Black Hills of South Dakota and encompassed both private and public land in Custer and Pennington Counties, including 286 km² in Custer

State Park. Elevations varied from 1108 m to 2208 m. Forested regions were prevalent at higher elevations and were dominated by ponderosa pine (*Pinus ponderosa*). Openings in the forest were created by logging, wildfire, and infestations of mountain pine beetle (*Dendroctonus ponderosae*). Lower elevations, especially the southeastern portion of the study area, were mainly composed of grasslands.

Average annual precipitation for our study area is 54.69 cm, and during our study average annual precipitation was 68.58 cm, 36.65 cm, and 61.29 cm for 2011, 2012, and 2013, respectively. Average annual temperature ranged from 6 °C to 9 °C across the study area (National Climatic Data Center 1981–2010). Road density was 2.1 km/km² in Custer State Park (CSP unpublished data) and averaged 3.2 km/km² in the Black Hills National Forest (T. Mills, Black Hills National Forest, personal communication).

Female elk were captured during February 2011–2013 by use of tranquilizer dart guns fired from helicopters. Elk were sedated using a butorphanol, azaperone, and medetomidine sedation protocol (Mich et al. 2008). During sedation, elk were blindfolded and equipped with a Global Positioning System (GPS) telemetry unit, which included a very high frequency (VHF) transmitter (Telonics Inc., Mesa, AZ.; Advanced Telemetry Systems Inc., Isanti, MN). GPS transmitters were set to collect satellite waypoints every 1.5–2 h daily. The South Dakota State University Research Committee approved all handling, marking, and monitoring procedures (Animal Care and Use Committee Approval Number 11-012A). When elk died or when collars were retrieved at the end of the study, GPS waypoints were downloaded for home range analysis. Chronic wasting disease (CWD) was present in our study area; however, no captured elk appeared affected by CWD and no CWD-attributed deaths were recorded (Lehman 2015). Female elk movements were monitored daily via VHF from May to August in order to determine parturition dates of marked females.

Home range (99%) and core area (50%) contours were estimated during summer and winter periods. Contours of 99% and 50% are commonly used to assess overall elk home ranges and core areas respectively for summer and winter ranges in our study system

TABLE 1. Summary of covariates thought to influence core area size of female elk in the southern Black Hills, South Dakota, from 2011 to 2013.

Covariates	Description
Year	
Open-canopied vegetation	Meadows and open-canopied forest with 0%–40% canopy cover (ha)
Moderate-canopied forest vegetation	Forest vegetation with 41%–70% canopy cover (ha)
Dense forest vegetation	Forest vegetation with >70% canopy cover (ha) and seedling/shrub (ha)
Roads	Road density (km/km ²)

TABLE 2. Summary of candidate models used to explain core area size of female elk during winter and summer in the southern Black Hills, South Dakota, from 2011 to 2013.

Model	Covariates ^a
1	Year
2	Open-canopied vegetation
3	Moderate-canopied forest vegetation
4	Dense forest vegetation
5	Roads
6	Year + Open-canopied vegetation
7	Year + Moderate-canopied vegetation
8	Year + Dense forest vegetation
9	Year + Roads
10	Open-canopied vegetation + Roads
11	Moderate-canopied vegetation + Roads
12	Dense forest vegetation + Roads
13	Global

^aDescriptions of covariates can be found in Table 1.

(Anderson et al. 2005, Benkobi et al. 2005, Ranglack et al. 2016). We based seasonal time periods on timing of parturition and also on vegetation conditions. Summer was defined as date of parturition through 31 October while winter was defined as 1 November to parturition the following year. These dates reflect primary plant growth and dormancy periods, respectively. For females that were barren or that aborted calves, we used the median date of parturition for each year as the start time for the summer season. Because elk in Custer State Park do not exhibit seasonal migrations and because much of the summer and winter home range boundaries overlap, no further designation of spring/fall home ranges was necessary (Millsbaugh 1995, Benkobi et al. 2005, Lehman 2015).

We used the BBMM package (Nielson et al. 2014) in program R (R Version 3.01.0, 2014, www.R-project.org, accessed 25 April 2015) to fit a BBMM to observed GPS locations of elk in space and time. The BBMM package provides an empirical estimate of the movement path of an animal using location data obtained at short time intervals (Horne et al. 2007). The Brownian bridge probability density connecting each pair of successive locations is an estimate

of the relative time spent in an area during the time interval between each location. Means, standard errors, motion variances, satellite error, and sizes of home ranges and core areas were estimated for summer and winter home ranges. ArcGIS 10.2 was used to evaluate the area of BBMM-generated contours (Esri, Redlands, CA). We compared elk home range size across years using an analysis of variance and the “*aov()*” function in R version 3.1.0 (R Development Core Team 2014) (R Version 3.1.0, 2014, www.R-project.org/, accessed 14 Mar 2016).

Core area contours were intersected with the Black Hills National Forest (BHNF) Forest Service Vegetation (FSVEG) Geographic Information System (GIS) coverage (BHNF unpublished data) and the CSP Land Cover GIS coverage (CSP unpublished data). Vegetation communities in GIS coverages were described using a hierarchical classification based on vegetation types and structural stages (Buttery and Gillam 1983). Forested stands were usually classified as seedling/shrub (<2.54-cm diameter at breast height [DBH]), sapling/pole (2.54–22.9 cm DBH), or mature/sawtimber (>22.9 cm DBH). The sapling/pole and mature/sawtimber forest stands were further classified into overstory categories of 0%–40%, 41%–70%, and >70% overstory canopy cover.

Appropriate vegetation structural stages were updated in GIS coverages for each year. National Agricultural Imagery Program (NAIP) imagery data (NAIP 13) were used to add private land polygons. We evaluated core area size in response to vegetation communities, road density, and year covariates (Table 1). We included the following vegetation community categories in our analysis: (1) open-canopied vegetation, which included both open-canopied forest (0%–40% overstory canopy cover) and meadows, (2) moderate-canopied forest vegetation (41%–70% overstory canopy cover), and (3) dense forest vegetation, which included forests with >70% overstory canopy cover and seedling/shrub stands.

TABLE 3. We report mean and standard error (in parentheses) for number of satellite locations, satellite error, motion variance, and Brownian bridge movement model (BBMM) home range (99% contour) and core area (50% contour) size in square kilometers (km^2) for both winter and summer seasons. Data were collected in the Black Hills, South Dakota, from 2011 to 2013.

Year	n	Satellite locations	Satellite error (m)	Motion variance	99% Home range size (km^2)	50% Core area size (km^2)
Winter						
2011	18	1180.67 (54.28)	23.15 (0.83)	839.63 (203.64)	35.70 (4.06)	3.26 (0.34)
2012	36	1797.75 (105.54)	18.07 (2.06)	739.59 (98.3)	40.04 (3.42)	4.21 (0.54)
2013	35	2636.37 (137.03)	17.81 (2.07)	615.52 (35.87)	44.76 (5.51)	4.21 (0.5)
Overall	89	2002.74 (90.86)	18.99 (1.18)	711.03 (45.67)	41.02 (2.67)	4.04 (0.3)
Summer						
2011	18	1777.94 (71.28)	32.34 (1.95)	1026.70 (112.71)	44.38 (4.3)	4.99 (0.51)
2012	35	2002.11 (82.16)	21.09 (2.65)	864.32 (53.48)	40.17 (2.56)	3.91 (0.36)
2013	35	2015.54 (79.42)	21.76 (2.75)	991.09 (99.9)	42.87 (3.91)	5.25 (0.56)
Overall	88	1961.60 (47.85)	23.66 (1.61)	947.9561 (50.02)	42.10 (2.01)	4.67 (0.29)

TABLE 4. Results of model selection for winter and summer core area sizes in response to covariates of influence in the Black Hills, South Dakota, 2011–2013. Only models with $\Delta\text{AIC}_c < 4$ are presented.

	AIC_c	ΔAIC_c	K	w_i
Winter model ^a				
Open-canopied vegetation + Roads	160.14	0.00	4	1
Summer model ^a				
Open-canopied vegetation + Roads	191.65	0.00	4	1

^aCovariates include open-canopied vegetation = meadows and open-canopied forest with 0%–40% canopy cover (ha), and roads = road density (km/km^2).

Road density was calculated by intersecting the GIS road coverages with core area contours in ArcGIS. Road density was expressed as road length (km) within a polygon over the area of the polygon. Also, year was evaluated as a variable to discern the effects of drought because 2012 received 67% of normal precipitation levels, and 2011 (125%) and 2013 (112%) were slightly above normal precipitation levels (National Climatic Data Center 1981–2010).

We used Akaike information criterion (AIC_c) adjusted for sample size to evaluate 13 different candidate models (Burnham and Anderson 2002; Table 2). Candidate models included underlying variables thought to influence core area size. We used 3 forms of covariates when first evaluating univariate models with a response variable of core area size: linear form, natural log form, and quadratic form (Franklin et al. 2000, Lehman et al. 2016). The linear covariate form indicated the lowest AIC_c score in a comparison of all 3 forms;

therefore, we used the linear form when fitting multivariate models (Franklin et al. 2000). Vegetative communities, road density, and year were included in multivariate models as potential factors affecting core area size.

We modeled elk core area size using linear regression with the “lme()” function in R version 3.1.0 (R Development Core Team 2014). The data set included several instances where core areas were evaluated for the same elk in sequential years, and we accounted for repeated measures using the linear mixed effects functions found in the “nlme()” package. We assessed model fit for the best-ranked model, using a coefficient of determination (R^2) diagnostic, as $R^2 = 1 - (\text{residual sum of squares}/\text{total sum of squares})$.

A total of 37 cow elk were included in our analyses from 2011 to 2013, resulting in a total of 88 summer home ranges and core areas and 89 winter home ranges and core areas (Table 3). Home range sizes did not differ by year for either winter ($F_{2,86} = 0.82$, $P = 0.44$) or summer periods ($F_{2,85} = 0.34$, $P = 0.71$; Table 3). The top-ranked model for both summer and winter seasonal core area sizes included open-canopied vegetation and road density (Table 4). Core area size increased with higher amounts of open-canopied vegetation ($t \geq 25.17$, $P \leq 0.01$) and higher road density ($t \geq 11.60$, $P \leq 0.01$) in both winter (Fig. 1) and summer (Fig. 2). Model fit assessments indicated that the top-ranked model fit our data well during winter ($R^2 = 0.96$, $P < 0.01$) and summer ($R^2 = 0.93$, $P < 0.01$). Core areas were roughly 12% the size of the 99% contours for both winter and summer periods.

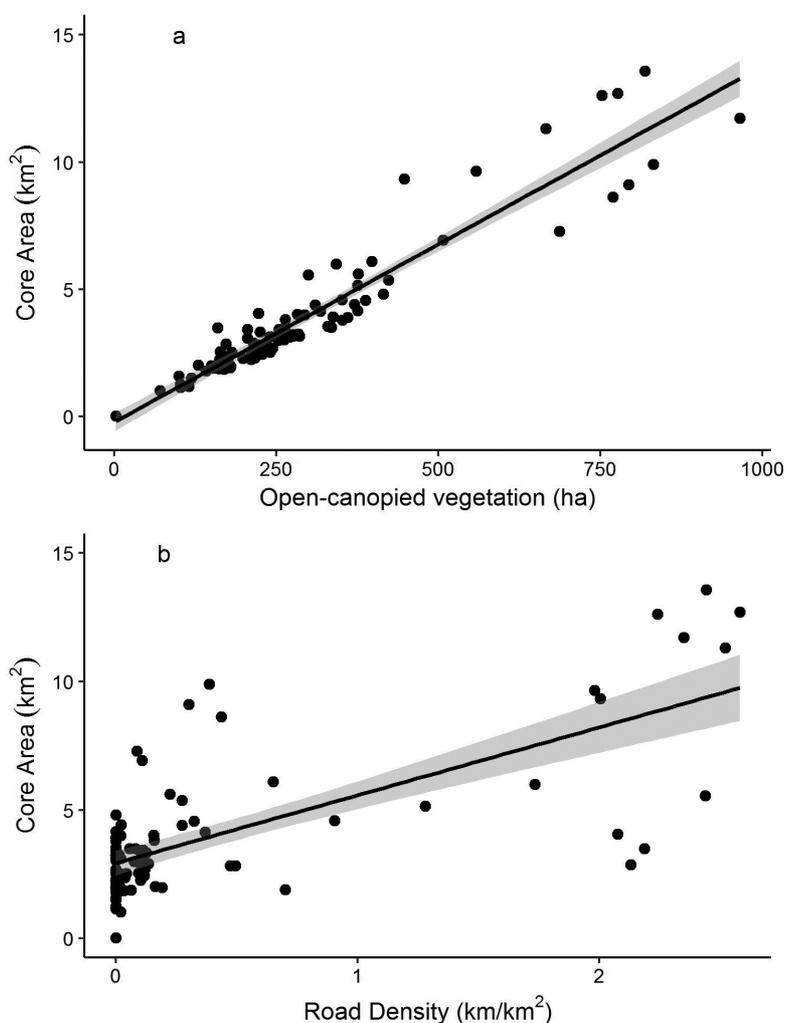


Fig. 1. Response of core area size (km²) as a function of open-canopied vegetation (ha of meadows and forest 0%–40% canopy cover) (panel a), and roads (km/km²) (panel b) from our best-ranked model during winter (1 November to date of parturition subsequent year) in the Black Hills, 2011–2013.

A small percentage of CSP elk home ranges were being utilized as core areas holding the majority of resources needed to fill the basic life requirements (Millspaugh 1995, Goldingay 2015). Both open-canopied vegetation communities and high road densities may explain the differences that we observed in overall space use by elk. Increased space use in open-canopied vegetation communities should be expected as elk travel from optimal foraging sites in open-canopied areas to ranges of increased security cover (Thomas et al. 1979).

As hypothesized, both road densities and open-canopied vegetative resources were

associated with an increase in core area size (Rumble et al. 2005, Montgomery et al. 2013). Negative effects of road networks on wildlife are widespread and can result in fragmented habitat, dispersal barriers, and increased human–wildlife interactions (Rowland et al. 2000, Dyer et al. 2001, Frair et al. 2008, Montgomery et al. 2013). Elk frequently select areas devoid of roads (Rowland et al. 2000, Benkobi et al. 2005), and altered ranges and movement patterns are common following human disturbance associated with roads in many ungulates (Rowland et al. 2000, Proffitt et al. 2013, Johnson and Russell 2014). Resources

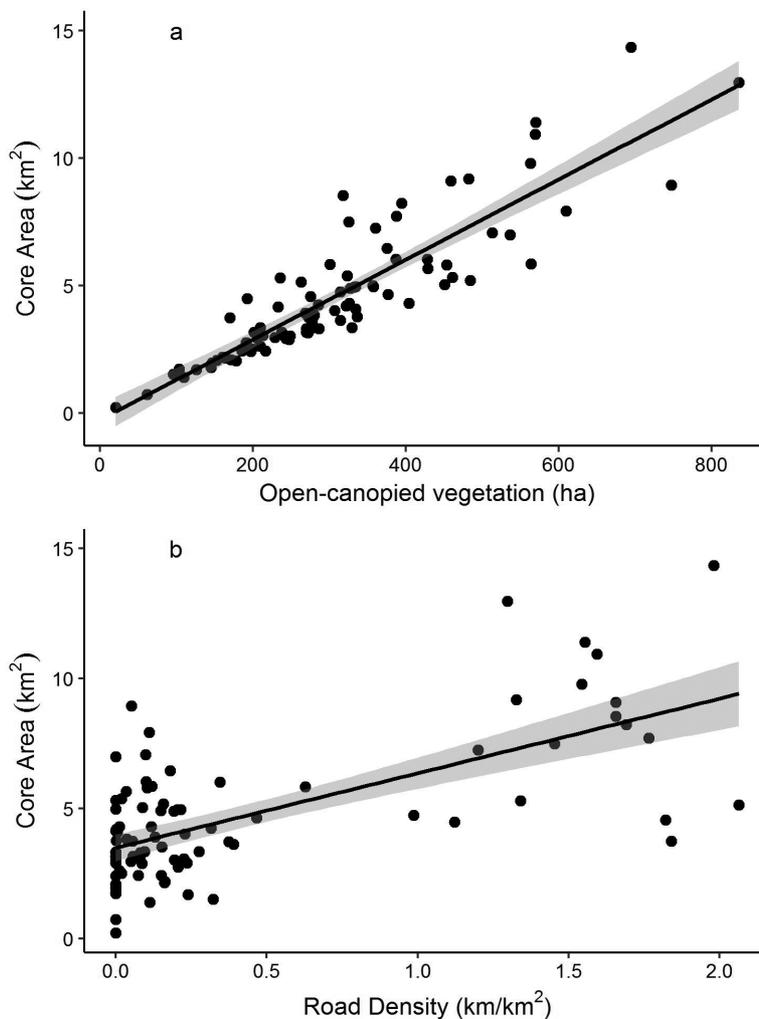


Fig. 2. Response of core area size (km^2) as a function of open-canopied vegetation (ha of meadows and forest 0%–40% canopy cover) (panel a), and roads (km/km^2) (panel b) from our best-ranked model during summer (date of parturition to 31 October) in the Black Hills, 2011–2013.

such as rugged terrain and vegetative cover can reduce the effects of road-related disturbances (Edge and Marcum 1991, Hillis et al. 1991, Millsbaugh et al. 2000, Rowland et al. 2000, Webb et al. 2011, Montgomery et al. 2012), yet use of these resources can vary given their proximity to road networks (Blan and West 1997, Millsbaugh et al. 2001, Rumble et al. 2005, Stubblefield et al. 2006, Sawyer et al. 2007, Montgomery et al. 2013). Environments devoid of roads are almost nonexistent in CSP, with no portion of elk home range habitats (>50th use contour) existing >1 km from at least a tertiary road (Montgomery et al. 2012).

Providing security cover for elk and an 800-m buffer of forest vegetation along roads as recommended by Hillis et al. (1991) could increase elk use of spaces near roads if vegetative cover were adequate (Montgomery et al. 2012).

Vegetative quantity and quality have been cited as primary factors determining space use requirements in ungulates (Christianson and Creel 2007, Esparza-Carlos et al. 2011, Morellet et al. 2013). Inherent in the home range theory is that an animal's life requisites are met by the resources available within its home range (Mitchell and Powell 2012), and life requisites are heavily prevalent in core

areas (Millsbaugh 1995). Elk strongly select for vegetation communities with greater herbaceous vegetation, such as open-canopied pine or aspen communities and grasslands, but avoid vegetation communities with high canopy cover, which provide less understory herbaceous vegetation (Rumble et al. 2007, Rumble and Gamo 2011). While open-canopied vegetation communities can produce high-quality foraging, open environments can lack security cover and protection from predation, harsh weather, and thermal radiation (Skovlin et al. 2002), which should be noted as a cost in optimal foraging theory described by Cook (2002) and Mitchell and Powell (2004, 2012).

Elk utilizing open-canopied communities might increase the size of their core areas to compensate for the depression in security cover resources (Mitchell and Powell 2004, Anderson et al. 2005). Inflated core areas can result in increased energy expenditure and increased potential of human-wildlife conflicts, and indicate a need for comparatively large conservation areas (Benkobi et al. 2005). Ecotones contrasting open-canopied vegetation communities with higher canopy cover are potentially high-use areas and result in (1) smaller home ranges due to optimal foraging opportunities and (2) lower energy expenditures to access security cover (Skovlin et al. 2002, Anderson et al. 2005). Use of vegetative cover as a disturbance buffer, especially along roads located near open-canopied areas, could be advantageous.

Despite a period of drought in 2012, our study found no difference in core area size among years. Vegetation communities, space use, and wildlife population densities can be modified by drought (Wang et al. 2002, Rivrud et al. 2010, Grovenburg et al. 2011). Cases of altered space use during or immediately following drought have been documented in elk (Singer et al. 1989), bighorn sheep (*Ovis canadensis*; Cain et al. 2008), mule deer (*Odocoileus hemionus*; Esparza-Carlos et al. 2011), and white-tailed deer (*Odocoileus virginianus*; Grovenburg et al. 2011). The number of investigations citing climate as a variable responsible for altering wildlife space use and movement is growing rapidly (Myserud 1999, Singh et al. 2012, Seebacher and Post 2015). Future evaluation of long-term drought effects could be beneficial in light of the predicted worsening of droughts over the 21st century (Duncan et al. 2012).

Climate, vegetative resources, and anthropogenic disturbance can influence wildlife space utilization and movement patterns, resulting in altered individual fitness (Morellet et al. 2013, Seebacher and Post 2015). Elk inhabiting open-canopied areas may increase their movements and home ranges in an attempt to find cover and avoid disturbance associated with roads. Implementing management strategies which mitigate human disturbance is especially important for areas with high road densities, as occurs in Custer State Park and the Black Hills, to reduce the likelihood of inflated core areas. We suggest that management provide forest vegetation buffers next to roads while also providing open-canopied forage resources to enhance optimal foraging opportunities and provide adequate security cover resources. Closing roads or limiting human disturbance in areas with optimal foraging resources may also enhance elk habitat.

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