Factors affecting spatial and temporal dynamics of an ungulate assemblage in the Black Hills, South Dakota

---

A Dissertation
Presented to
The Faculty of the Graduate School
At the University of Missouri

In Partial Fulfillment
Of the Requirements for the Degree
Doctor of Philosophy in Fisheries and Wildlife Sciences

By
BARBARA JEAN KELLER
Dr. Joshua J. Millspaugh, Dissertation Supervisor

JULY 2011

The undersigned, appointed by the dean of the Graduate School,

have examined the dissertation entitled

FACTORS AFFECTING SPATIAL AND TEMPORAL DYNAMICS OF AN UNGULATE ASSEMBLAGE IN THE BLACK HILLS, SOUTH DAKOTA

Presented by Barbara J. Keller

A candidate for the degree of

Doctor of Philosophy in Fisheries and Wildlife Sciences

And hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Joshua J. Millspaugh

Dr. Frank R. Thompson

Dr. Mark Ryan

Dr. John Kabrick

Dr. Gary Brundige

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Joshua Millspaugh, for giving me the opportunity to pursue my doctorate at the University of Missouri. I could not have asked for a better mentor, advisor, and teacher. This project would not have been possible without the guidance and support of Dr. Gary Brundige of Custer State Park. My committee members, Drs. Brundige, Thompson, Kabrick and Ryan, provided helpful guidance and comments throughout the dissertation writing process. I appreciate their time and patience throughout out my graduate career.

There were many individuals from Custer State Park that made my field research possible. Everyone at the resource office, including Dr. Chad Lehman, Bill Hill, Chad Kremer, Brenda Hall, and Adam Gahagan, were especially helpful. The staff at the park shop, especially Blake Clark and Roger Steinhour, were always willing to help with equipment issues and stuck or broken-down field vehicles.

Numerous technicians and volunteers played a part in my field research. They include the Painters, Katie Baumann, Cory Mosby, Cliff Sunda, Bryan Voelkner, Alyce Johnson, Chris Hansen, Kelly Mottaz, Emily Hockman, Kelly Asbill, Wes Hoyer, Joe Winski, and Preston Feltrop. Dr. Lowell Schmitz and John Kanta from the South Dakota Department of Game, Fish and Parks helped with pronghorn capture and handling. Dr. Chad Sexton, from Theodore Roosevelt National Park, taught me diet analysis techniques. Bill Dijak from the USFS provided invaluable GIS support.

Former and current members of the Millspaugh lab, including Robert Gitzen, Chadwick Rittenhouse, Kimberly Suedkamp Wells, Tom Bonnot, Damon Lesmeister, Chris Hansen, Jesse Kolar, Remington Moll, Cathy Bodinof, David Jachowski, Jaymi

Lebrun, Chris Rota, Stephanie Zimmer, and Amy Bleisch provided feedback, moral support and friendship throughout my graduate career. I especially thank Dr. Robert Gitzen for statistical assistance and advice.

I simply would not have made it through this process without the moral support of my friends and family. I thank my mother, Brigid Keller, for instilling in me a value for education, and for giving me opportunities she never had. Thanks to my sisters, Kathleen Whitney and Dr. Peggy Keller, for serving as incredible role-models during my youth and throughout my graduate career. I thank my fellow graduate students, especially Cara Joos and Morgan and Walter Wehtje, for valuable distractions from dissertation writing and commiseration over the trials and tribulations of graduate school. Without the support of Edward Bulliner, I likely would have lived in absolute squalor during the last few months of graduate school. Thanks everyone!

PREFACE

The goal of my dissertation was to assess and model the factors affecting temporal and spatial selection of resources by the large herbivore community in Custer State Park (CSP), South Dakota. The first step in my research was to determine forage availability and the factors that affect forage biomass (Chapter 1). I used this model of forage biomass in an evaluation of the spatial selection of resources by bison (Chapter 2) and pronghorn (Chapter 3), which I used in conjunction with previous resource selection studies of elk, mule deer and white-tailed deer in CSP to evaluate where animals occur and co-occur on the landscape and mechanisms which influence those relationships (Chapter 5). I also evaluated diet composition and overlap among the ungulate community (Chapter 4). This research culminated in a spatially-explicit model that I designed as a tool for managers to determine stocking densities for the ungulate assemblage (Figure 1). Throughout this dissertation, I attempted to provide results applicable to managers, but when possible, also answer broad theoretical questions about ungulate ecology in CSP.

My dissertation consists of 6 chapters: Chapter 1 describes forage composition in CSP and the spatially-explicit predictive biomass model; Chapters 2 and 3 are studies of the factors affecting bison and pronghorn resource selection, respectively; Chapter 4 evaluates diet composition and overlap of the ungulate assemblage; Chapter 5 evaluates the mechanisms affecting habitat overlap of the ungulate assemblage; and Chapter 6 is a description of the forage allocation model that incorporates information from each preceding chapter (Figure 1). Each chapter in this dissertation builds in complexity towards a greater understanding of the selection of resources by, and the relationships between, the ungulate assemblage in CSP.

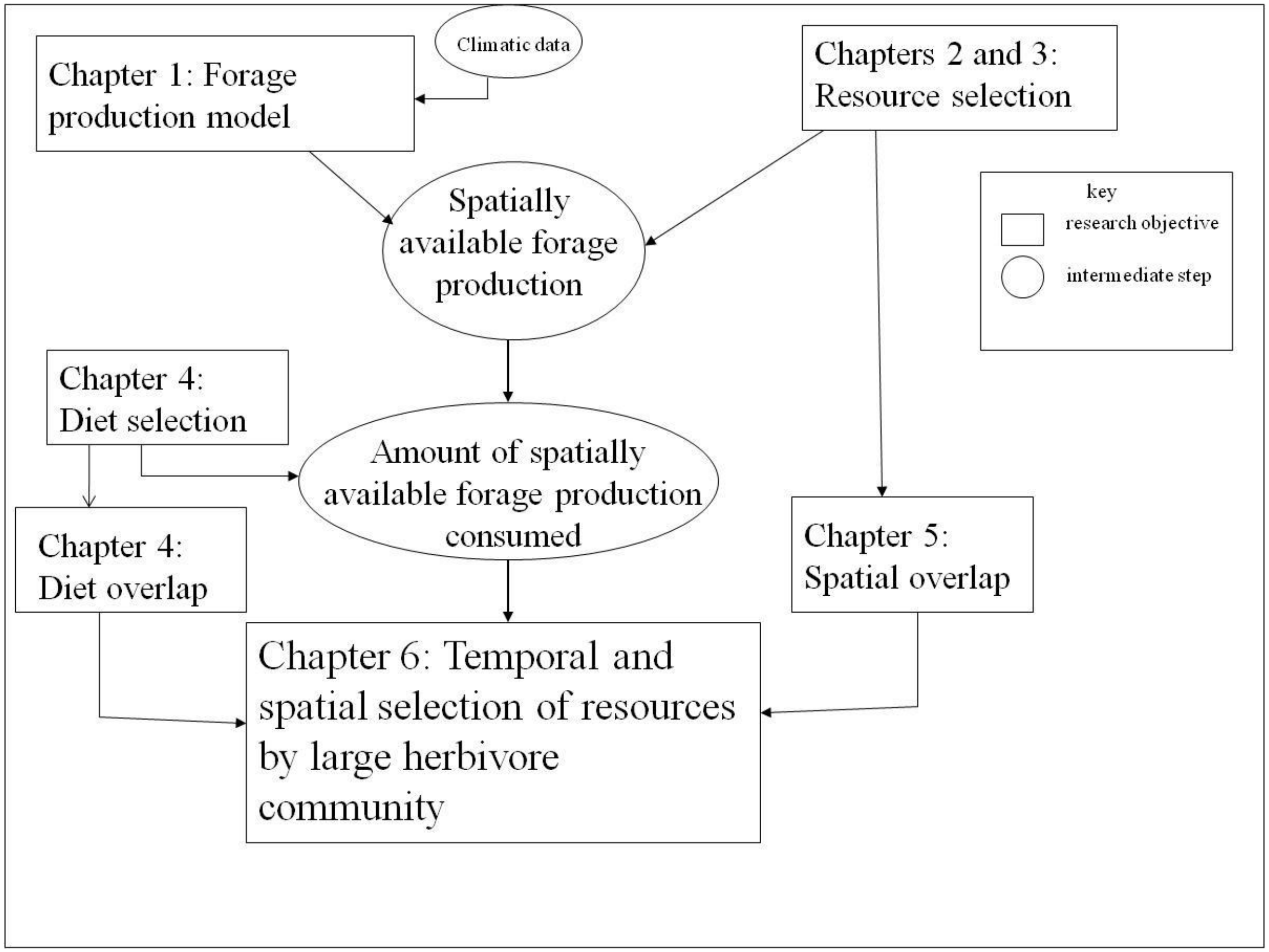

Figure 1. Flowchart displaying integration of research objectives and intermediate steps in the Keller (2011) dissertation.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I.

CHAPTER II.

CHAPTER III.

CHAPTER IV.

CHAPTER V.

CHAPTER VI.

LIST OF FIGURES

CHAPTER I.

CHAPTER II.

CHAPTER III.

CHAPTER IV.

CHAPTER V.

CHAPTER VI.

ABSTRACT

The Great Plains of the United States is an area of historically high ungulate species diversity. Large roaming herds of bison (*Bison bison*) once coexisted with pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) and the now extinct Audubon bighorn sheep (*Ovis canadensis* auduboni) on the open range. A few parks and preserves, scattered across the northern Great Plains and the American west, still maintain the remaining ungulate assemblage. In many of these parks, natural processes such as large-scale migration and population regulation by large predators no longer occur. Management of these closed populations is critical to prevent overutilization of the rangeland. An understanding of the spatio-temporal selection of resources by the ungulate community is key to develop management actions, such as culling plans.

Custer State Park (CSP), South Dakota, manages the full suite of ungulates native to the Great Plains for wildlife viewing, hunting, and other purposes. Management is based on untested assumptions regarding forage production, and resource selection and overlap of the ungulate assemblage. Our goal was to gain empirical data on the spatial and temporal selection of resources by the ungulate assemblage in CSP. To achieve this goal, we developed a spatially-explicit model to predict forage production throughout the park, evaluated factors affecting bison and pronghorn spatial selection of resources, evaluated diet selection and overlap among the ungulate assemblage, and habitat overlap among the ungulate assemblage. We incorporated this information into a spatially-explicit linear optimization model which estimated optimal stocking densities for CSP.

The best model to predict forage production included spring precipitation, previous year spring precipitation, range/woodland site, canopy cover, elevation, and whether a site was a prairie dog (*Cynomys ludovicianus*) colony. This model explained 40% of the variability in biomass production. Palatable species production was lower than total biomass produced and ranged 82–99% of total production for range and woodland sites. Our forage production model predicted 28,499,216 kg of palatable forage was produced in a year of average spring precipitation (208 mm) and date of last spring frost (11 May).

We observed considerable individual heterogeneity in the mechanisms affecting bison and pronghorn resource selection. In general, we found that forage biomass was most important to bison and pronghorn resource selection in CSP, but only when placed in the context of unique seasonal stressors, such as water and human disturbance. During every season, female bison occurred in areas that support high forage biomass, including the mixed-grass prairie and upland shrubland habitat types in CSP. However, differences in seasonal selection did occur. Female bison selected areas close to mineral sites during winter and spring, areas away from unpredictable disturbances during the spring, and areas close to ponds during the summer. Male bison also selected areas of high forage biomass during the non-breeding season, but occurred further from mineral sites and ponds, and close to streams. Although the high amount of heterogeneity and low sample size of male bison resource selection resulted in low predictive ability of population-level

probability of occurrence maps, the probability of occurrence maps for female bison performed well based on *k*-fold cross-validation. These results indicate bison herds are likely to change foraging patterns in relation to unique seasonal stressors and changes in palatable forage availability. Limiting the amount of unpredictable disturbance, or allowing disturbance-free areas, during the calving season may be beneficial to female bison with young.

During most seasons, pronghorn selected areas of high forage biomass close to ponds and far from streams. Pronghorn also reacted to seasonal changes in human disturbance; during the fall and spring pronghorn selected areas of high forb biomass that were close to human disturbance, but during the winter and summer, selected areas of high forb biomass away from human disturbance. Areas of high use during spring and winter were more concentrated than during summer and fall. In general, predicted pronghorn use was highest in the area of Custer State Park occupied by mixed-grass prairie, but also was high in portions of fire-killed forest. Management and conservation of pronghorn populations should focus on forage production, but also consider human disturbance and the types of water sources that are available. Further, the amount of heterogeneity we found in both bison and pronghorn resource selection suggests analyses that pool locations across individuals will likely miss the full suite of factors affecting resource selection of ungulates, including gregarious species that form large groups.

We used microhistological techniques to estimate diet composition of each ungulate species, and calculated Schoener's index of dietary overlap, which ranges from 0 (complete separation) to 1 (complete overlap), between each species pair. Diet composition of each species followed *a priori* expectations based on the physiology and natural history of the species. Bison were bulk grazers; annual diets consisted primarily of cool-season grasses (57.9%), warm-season grasses (21.7%), and sedges (15.4%), and only small amounts (4.9%) of shrubs and forbs. Elk fed intermediately on grass and forbs and shrubs; annual diets consisted of primarily grass (63.1%), and moderate amounts of shrubs (25.7%) and forbs (10.2%). However, during spring grass composition was > 80% of elk diets; elk may be considered bulk grazers during this time period. Pronghorn, mule deer, and white-tailed deer were concentrate selectors. Annual pronghorn diets were primarily split between forbs (48.2%) and shrubs (40.4%), and grasses made up 9.8% of their diet. Mule deer diets were predominately shrubs (72.7%) although forbs were important as well (22.9%); grasses made up only 5.1% of mule deer diets. White-tailed deer consumed more grass than the other concentrate selectors, with an annual diet composition that was 28.7% grass; however shrubs dominated their diets (55.1%) and forbs were an important component (16.2%). Overall, annual dietary overlap was high between bison and elk (0.63), elk and white-tailed deer (0.60), pronghorn and mule deer (0.61), and white-tailed deer and mule deer (0.55). Annual overlap was lowest between bison and mule deer (0.08) and bison and pronghorn (0.16). In general, dietary overlap among ungulate species was greatest during the summer and lowest during the winter.

Habitat overlap among all species was highest during winter and lowest during the summer. Female bison and pronghorn, both sexes of bison and elk, and white-tailed deer and elk used habitat in a similar manner during most seasons. For all seasons except

summer, habitat overlap was most associated with high forage biomass and water at the edges of habitat patches. During fall and winter, habitat overlap among all species increased at areas of high forage biomass and diversity and areas of high patch edge density. During spring, habitat overlap among all species increased near intermittent streams at areas of high patch edge density. During summer high habitat overlap among all species was found close to intermittent streams, and away from flowing streams and ponds. Our data are consistent with the hypothesis that coevolutionary divergence or competition has resulted in habitat partitioning among the ungulate assemblage, with overlap among ungulates occurring at high quality resources within these habitat patch edges.

We used spatially-explicit information of forage production, diet selection, space-use, and habitat overlap of an ungulate assemblage gained during our study to develop a model that used linear optimization to optimize stocking densities of bison, elk, pronghorn, mule deer, and white-tailed deer. Seasonal carrying capacity estimates incorporating all factors were highest during the winter (2864 ungulates), intermediate during spring (1636 ungulates) and fall (1353 ungulates), and lowest during the summer (1012 ungulates). Our model optimized seasonal stocking densities at 25% allocation of total forage production at 500–659 bison, 212–699 elk, 100–584 mule deer, 100–795 white-tailed deer, and 100–541 pronghorn, which were generally below current stocking densities for most species. Comparison of current stocking densities to forage production suggest utilization of many forage species may be above 25% but generally below 50%. In general, tradeoffs existed between maximizing bison and elk, elk and white-tailed

deer, and pronghorn and mule deer populations. Coexistence of bison and elk populations was dependant on the availability of palatable grasses, while forbs and shrubs were important for white-tailed deer and elk, and mule deer and pronghorn. Forage species that our model indicated have a tendency to be overutilized at current stocking densities include big bluestem (*Andropogon geradii*), blue grama (*Bouteloua gracilis*), needleanthread (*Stipa comata*), sedges (*Carex* spp), common yarrow (*Achillea millefolium*), northern bedstraw (*Galium boreale*), and woodland shrubs. Management actions that increase the biomass of these species would facilitate coexistence among the ungulate assemblage. Our results demonstrated the importance of incorporating diet overlap, habitat overlap, and resource selection in stocking density estimates, especially for large and diverse ungulate assemblages. The model we produced will be most useful to examine theoretical relationships related to stocking densities and forage production, and tradeoffs in optimizing ungulate population numbers, rather than a strictly applied estimate of ungulate carrying capacities.

CHAPTER I. A SPATIALLY EXPLICIT FORAGE PRODUCTION MODEL FOR A MIXED-GRASS PRAIRIE AND PONDEROSA PINE WOODLAND IN THE BLACK HILLS, SOUTH DAKOTA

ABSTRACT

Wildlife stocking-rate decisions are critical to the long-range stability of range ecosystems and depend on accurate estimates of forage production. Decision-support tools, such as forage production models, can be especially important to land management in the Northern Great Plains, where climate is variable and drives forage production. Natural Resource Conservation Service (NRCS) production tables are important tools for range managers because they estimate forage production by soil units and do not require substantial time or money. Custer State Park (CSP) estimates annual forage production, which dictates wildlife stocking rates, using a model that incorporates NRCS estimates. CSP modifies these estimates with a moving-two-year mean of annual precipitation. However, this modified NRCS model relies on several un-tested assumptions. It is necessary to determine the efficacy of this model and assess whether other model formulations are appropriate. Our objectives were to measure forage production in CSP and develop a spatially explicit model to predict species-specific biomass, as well as woody twig and foliage biomass, and compare estimates from this model to the modified NRCS-based model used by CSP as well as unmodified NRCS estimates. We used clipping and weighing and visual obstruction techniques to measure forage biomass in

CSP and adjoining Wind Cave National Park, 2005–2008. We used stratified sampling based on range and woodland grazable site, and refined sampling based on power analyses using 2005 field data. We used a repeated measures, mixed-effect model to predict spatially-explicit biomass production. The best model to predict forage production included spring precipitation, previous year spring precipitation, range or woodland site, canopy cover, elevation, and whether a site was a prairie dog (*Cynomys ludovicianus*) colony. This model explained 40% of the variability in biomass production. Palatable species production was lower than total biomass produced and ranged 82–99% of total production for range and woodland sites. Our forage production model predicted 28,499,216 kg of palatable forage was produced in a year of average spring precipitation (208 mm) and date of last spring frost (11 May).

We compared our forage production model to the modified NRCS model used by CSP and to unmodified NRCS estimates. The composition of warm and cool-season, shrub, and forb communities did not match NRCS-expected distributions for any of the range sites. The unmodified NRCS estimates were the least accurate method to predict forage biomass in CSP. The unmodified NRCS estimates on average under-predicted biomass at each sampling site by 410 kg/ha, and deviated a total of 1,328.4 kg/ha from observed biomass on average. The modified NRCS and empirical models produced similar estimates of biomass. The empirical-based forage production model predicted 16 to 28% less biomass than the modified NRCS forage model using climate conditions specific to 2005 and 2006; but predicted 15 to 25% more biomass than the modified NRCS forage model using climate conditions specific to 2007 and 2008. Using climatic attributes for an "average" year, the empirical model predicted 9.5% more biomass than the modified NRCS model. In general, the modified NRCS model predicted higher biomass in areas of steep slope compared to the empirical model, whereas the empirical model predicted higher biomass under areas of canopy cover compared to the modified NRCS model. Despite these differences, there might be advantages to using both forage models when making management decisions. The empirical forage model incorporates continuous modifiers of slope and canopy cover, and does not require labor-intensive condition surveys, whereas the modified NRCS model incorporates field-based and site-specific range condition ratings. We think the modified NRCS model likely gives a better estimate of production within the deferred grazing pastures, as we did not stratify sampling by pastures to create the empirical model. We recommend the modified NRCS model be used to estimate production in the silty footslope, stony hills, and thin upland range and woodland sites, and the empirical model be used to estimate forage production in all other range and woodland sites. However, because the empirical forage production model estimates species-specific forage production, it is more useful for estimating ungulate carrying capacity or for any other purpose that requires species-specific data.

INTRODUCTION

Available forage biomass is the main determinant of stocking rates and carrying capacity estimates for domesticated and wild herbivores, and is a function of both abiotic (e.g., precipitation, temperature, elevation) and biotic (e.g., organic matter, canopy cover, grazing history) factors (Wight and Hanks 1981, Wight et al. 1984, Milchunas et al. 1994). The interactions among these factors and how they influence forage production is complex and spatiotemporally dynamic. Models are often used to predict annual biomass and elucidate relationships between environmental attributes and biomass production (Howe 1994, Andales et al. 2006) to aid in management decisions.

Many land managers base biomass estimates or models on production tables derived by the National Resource Conservation Service (NRCS). The NRCS publishes soil surveys and production estimates that can be modified for unfavorable, average, and favorable climatic conditions and for range condition (poor, fair, good, excellent) based on species composition (National Resource Conservation Service 2002). Despite their frequent use, NRCS estimates are rarely tested and do not account for variability in spatial factors such as slope, aspect, and elevation within soil map units or range and woodland sites. The NRCS model might also oversimplify the effects of precipitation on production because it only considers current annual precipitation, and does not account for differences in seasonal precipitation or the length of the growing season. Given these issues, empirical measurements of forage biomass and an evaluation of factors affecting biomass production should occur if management goals are to maintain a sustainable grazing system.

Recent advances in forage production modeling include complex simulation models (SPUR, SPUR2, GPFARM, PHYGROW) which require information on soil water, plant respiration rates and plant senescence among other factors (Wight and Skiles 1987, Andales et al. 2005 and 2006, Jama et al. 2006). These models are typically applied and tested on fairly small uniform (i.e., low soil variability) pastures (Andales et al. 2005 and 2006) and thus have not been applied to large and diverse landscapes. Biomass estimation via remote sensing is also increasing in use (Xie et al. 2009); however, its application is limited to grassland areas and does not perform well for understory herbage production in woodland or shrub communities (Wylie et al. 1996, Mirik et al. 2006). A landscape-level model to predict forage biomass in an area of diverse topographic and soil features as well as under a dense canopy cover, to our knowledge, does not exist.

Resource managers in Custer State Park (CSP), SD, currently estimate range carrying capacity for wild ungulates (principally bison (*Bison bison*) and elk (*Cervus elaphus*)) using a model that incorporates precipitation levels and NRCS estimates of forage production per soil map unit. Managers use a moving-mean of precipitation that accounts for the previous and current year precipitation and the deviation from normal precipitation patterns (G. Brundige, personal communication, CSP). This moving mean is used in place of the 'average, unfavorable and favorable' NRCS modifiers to predict forage production. Managers must also predict forage production for soil types that are not included in the range and woodland sites in the NRCS production tables. For example, the woodland site 'steep rocky side slope' makes up 22% of the park, yet NRCS estimates do not provide data on forage production for this site because the slopes are steeper than what domestic cattle typically graze. Wild ungulates, however, utilize steeper slopes than domestic livestock (Stewart et al. 2002), and the managers must make gross estimates of forage production on these steeper sites from available data for production on 'rocky side slope'. Further modification of biomass is made using range condition modifiers for each range site based on field estimates in different pastures in CSP. Forage production estimates for CSP using this model remain untested. Decisions based on these production estimates have a significant impact on habitat condition and directly influence hunting and culling quotas (stocking rates) of bison and elk and other ungulate species.

Our goal was to construct a spatially explicit forage production model for CSP based on empirical data, and to compare biomass estimates from this model to the NRCS model currently used by CSP. To reach this goal, our objectives were to 1) measure species-specific forage production; 2) use environmental and climatic attributes to build a model that predicts biomass in a spatially-explicit manner; 3) estimate shrub twig and foliage biomass; 4) incorporate the models into GIS to predict forage production at a resolution of 30 × 30 m throughout CSP; and 5) compare biomass predictions from the empirical-based model to the modified NRCS-based model and to unmodified NRCS estimates.

STUDY AREA

Custer State Park encompasses 286.32 km^2 in southwest South Dakota, and is composed of a mixture of rangeland and forest common to the southern Black Hills region. Steep granite spires characterize the northwest portion of the Park, undulating forested hills dominate the central portion, and grasslands dominate the eastern and southern portions of the Park (CSP 1995; Figure 1). Elevations range from 1,146–2,042 meters (CSP 1995).

Over half (55%) of CSP is covered by forest. The central forested portion of CSP is dominated by ponderosa pine (*Pinus ponderosa*) which shifts to a mixture of ponderosa pine and white spruce (*Picea glauca*) on northern slopes and high elevations (Figure 1). A small amount of deciduous forest (2% of CSP) is characterized by predominantly bur oak (*Quercus macrocarpa*) and paper birch (*Betula papyrifera*) forest occurs primarily in riparian corridors (Figure 1). Stand structure diversity in CSP consists of 5,233 ha of single-story forest and 71.49 km^2 of multi-story forest (CSP 1995). Woodland understory communities in CSP are dominated by Kentucky bluegrass (*Poa pratensis*), poverty oatgrass (*Danthonia spicata*), sedges (*Carex* spp.), bearberry (*Arctostaphylos uva-ursi*), wild raspberry (*Rubus ideaus*), and western snowberry (*Symphoicarpus occidentalis*; Custer State Park, unpublished data). Almost 30% of CSP is burned-over forest, the results of the Galena fire of 1988, the Cicero Peak fire of 1990, and the Four-mile fire of 2008. Fire-damaged forest consists of 109.79 km^2, 60% of which is fire-killed where the canopy remains primarily open (CSP 1995; Figure 1).

Approximately 21% (61.05 km^2) of CSP is northern mixed-grass prairie and upland shrubland (CSP 1995; Figure 1). Grasslands are dominated by Kentucky bluegrass, big bluestem (*Andropogen gerardi*), little bluestem (*Andropogen scoparius*), western wheatgrass (*Agropyron smithi*), blue grama (*Bouteloua gracilis*), and sideoats grama (*Bouteloua curtipendula*; CSP 1995). Common shrub species include leadplant (*Amorpha canscens*), western snowberry, wild raspberry, and wild rose (*Rosa* spp.).

There are 12 range and woodland grazable sites in CSP (Figure 2): rocky side slope (226.80 km^2; 46.1% of CSP), stony hills (52.00 km^2; 10.6%), overflow (23.80 km^2; 4.8%), silty (14.90 km^2; 3.0%), cool slope (12.10 km^2; 2.5%), warm slope (12.10 km^2; 2.5%), shallow ridge (8.10 km^2; 1.6%), clayey (7.40 km^2; 1.5%), shallow (7.20 km^2; 1.4%), savannah (5.50 km^2; 1.1%), silty footslope (0.90 km^2; 0.2%), and thin upland (0.20 km^2; <0.1%). Park managers created 3 woodland grazable sites that were not included in NRCS production tables due to the steepness of slope (Figure 2): steep rocky side slope (107.10 km^2; 21.7% of CSP), steep cool slope (0.23 km^2; 0.5%), and steep warm slope (12.00 km^2; 2.4%). Soil Conservation Service (1990) provides descriptions of range and woodland grazable sites in CSP.

For 1992–2008, annual precipitation based on the water year (1 October – 30 September) for CSP averaged 498.6 mm and ranged from 74% to 161% of the 25-year mean. Approximately 76% of precipitation in CSP falls from April to September (Custer State Park, unpublished data). During our study period, 2005–2008, the average annual precipitation was slightly lower than normal at 439.9 mm, and ranged from 78.2% to 106.2% of the 25-year mean. Spring precipitation (1 April – 30 June) was also normal and above average for 2005 and 2008, when it was 96 and 129% of the 25-year mean, but much below average during 2006 and 2007, when it was only 67 and 68% of the 25-year mean, respectively. Winter in the southern Black Hills is considerably milder than elsewhere in the region, and a persistent snowpack was not typically present during the study period. Average snowfall for the southern Black Hills is 3200 mm; March is the snowiest month with an average snowfall of 1880 mm. Temperatures in CSP are also more moderate than the surrounding plains; the average annual, summer and winter temperature in CSP is 6.7° C, 16° C, and –5° C, respectively (CSP 1995).

Approximately 800–1000 bison, 408–718 elk, 163–279 pronghorn *(Antilocapra americana*), 867 white-tailed deer (*Odocoileus virginiana*), 285 mule deer (*Odocoileus hemionus*), and 38–48 bighorn sheep (*Ovis canadensis*), and 35-40 feral burros (*Equus asinus*) occupied CSP during our study period (C. Lehman, Custer State Park, personal communication). Bison are culled annually during the fall bison roundup, as well as during several hunts in the fall. A 1.54 m woven-wire fence surrounds the majority of the CSP except for a small portion of the Park in the Needles and Sylvan Lake area and the

Stockade area. This fence prevents movement of bison but allowed for movement of all other ungulate species into or out of CSP, although movement of ungulates out of the park is rare (CSP, unpublished data). There are three other internally fenced areas in CSP, which create three distinct pastures in CSP and are used to move bison during the roundup and to manage grazing of bison throughout the year (Figure 1).

METHODS

Sampling

Clipping and Weighing. We used the clipping and weighing technique to estimate forage production throughout CSP (Higgins et al. 1994). This technique is generally considered the most accurate technique for biomass estimation (Higgins et al. 1994, Olenicki and Irby 2005). We stratified our sampling based on range and woodland grazable sites in CSP (Figure 2). A range site is a grouping of soil map units that "produce about the same kinds, amounts, and proportion of native vegetation" (Soil Conservation Service 1990; pp 90). Generally, soil units that produce similar plant communities are grouped into range sites, or woodland grazable sites when forest is the present or potential land use (Natural Resource Conservation Service 2002). We conducted a pilot study during the summer and fall 2005 to determine the number of clipping sites needed per range and woodland site. We clipped 150 sites, stratified as 10 sampling sites per 15 range or woodland soil sites. We randomly located 10 sampling sites (0.25 m^2) per range site using the Hawth's Tools extension for ArcGIS 9.0 (Beyer 2004). Based on a power analysis (power = 0.8, $\alpha = 0.05$) of the results from biomass clipping in fall 2005, we selected an additional 101 sites in 2006 at range and woodland sites that were undersampled. In 2008 we selected an additional 41 sampling sites to replace damaged sampling plots, and selected 80 sampling sites in Wind Cave National Park (WICA), located directly south of CSP. We sampled in WICA as part of separate forage production modeling effort for that park, and because the study areas were adjacent to one another we included those sampling sites in our analysis to supplement our sampling in CSP. We clipped 150, 156, 92, and 351 biomass sampling sites in 2005, 2006, 2007 and 2008, respectively (Figure 1).

We erected grazing-exclusion cages that were 1.17 m^2 area and 1.0 m height, constructed of circular welded wire fencing panels, at each sampling site to prevent the removal of biomass by grazing ungulates. We secured the cages using four 15–33 cm tent stakes. We did not specify distances between sampling sites within or between different range or woodland sites, or limit the number of cages per patch. Rather, we used stratified random sampling to locate sites. We downloaded the site locations into a handheld GPS unit for navigation in the field. For wooded sites, we placed cages in the area closest to the randomly generated point with minimal to zero canopy cover. Because the relationship between canopy cover and herbage production is well documented (Woods et al. 1982, Bennett et al. 1987, Moore and Deiter 1992), and the actual forage production of woodland sites in CSP is less documented, we selected areas that would limit the influence of canopy cover on our production estimates. In doing so, we gained a better estimate of the true production potential of each woodland site. However, because we were not always able to identify an area of zero canopy cover in close proximity to the pre-determined site location, we placed sampling sites under the area of most minimal canopy cover that was within the particular range or woodland grazable site patch.

We visited cages in late summer and fall (August 1—November 1) each year (2005–2008) to measure biomass, however, due to damage to cages and budget limitations we were unable to sample all sites every year; we sampled 100, 96, 57, and 97%, of cages 2005–2008, respectively. Numerous studies of forage production in the northern mixed-grass prairie report that peak standing biomass occurs between early June and mid-July (Lauenroth and Whitman 1977, Sims and Singh 1978, Dodd et al. 1982, Heitschmidt et al. 1995). Although we undoubtedly missed some amount of warm-season production for cages that were clipped earlier in our sampling period, and perhaps underestimated production late in the sampling period due to desiccation from weather events and insect and small mammal herbivory, we could not visit and clip each sampling site within a shorter time period. We attempted to vary the area and range sites we visited day-to-day so that all sampling sites of one range site were not clipped early in the sampling period, to avoid biasing biomass estimates. Due to trampling by bison and damage from other wildlife and weather, some cages were destroyed throughout our study. We did not clip damaged cages and replaced them if possible.

Double Sampling. In addition to clipping and weighing we used a double-sampling procedure using visual obstruction (Benkobi et al. 2000) and ocular coverage estimates to predict forage production. We used modified Robel poles (visual obstruction poles; Benkobi et al. 2000) to relate visual obstruction to standing biomass. Our visual obstruction poles consisted of 1 m of PVC pipe striped with alternating gray and white bands (2.54 cm wide), numbered from the bottom of the pole 0–50. A rope 4 m in length connected the top of the numbered pole to a plain pole of the same height. At each sampling site clipped for biomass, we placed the numbered pole in the center of the plot before clipping. An observer, holding the plain pole, read the lowest visible number on the pole from a length of 4 m and a height of 1 m, while the recorder held the numbered pole in place. We averaged visual obstruction readings from 4 cardinal directions at each site (Benkobi et al. 2000). Beginning in 2006, in addition to visual obstruction, we also recorded percent coverage of total herbaceous cover and bare ground at each sampling site.

Site Attributes and Weighing. Before we clipped or measured visual obstruction at each site we measured percent slope with a clinometer, determined aspect, and measured canopy closure with a spherical densitometer. We clipped a 0.25 m^2 plot of all vegetation within each cage (Figure 3). We separated plants by species during clipping to determine species-specific production at each site. After clipping, we moved the grazing-exclusion cage adjacent to the clipped site to avoid the effects of clipping on the forage production estimate for the next field season. We moved the cage approximately1.2 m, in a different direction each field season (east in 2005, north in 2006, west in 2007) so our browse measurement plots did not overlap among seasons (see browse methods below). Because the location of one cage during the 2006, 2007 and 2008 field seasons depends on the location of the cage in the 2005 or previous field season, only one field season was a true stratified-random sample. Although this may be characterized as pseudoreplication, we believe comparing production estimates at the same sites among years allowed a more accurate estimate of the effect of precipitation and other temporal variables on forage production (Ratti and Garton 1994). We dried clippings in an oven at 90°Celsius for 48 hours and weighed each species to the nearest 0.1 g.

Shrub production. At each clipping site, we also clipped any new twig or leaf growth on any shrub species (Larson and Johnson 1999) occurring within a 25 m^2 or 6.25 m^2 plot placed around each cage (Figure 3). A larger plot is needed to estimate browse biomass since browse production occurs at a larger scale than understory herbage production (Higgins et al. 1994). We clipped all shrub and tree browse within 1.83 m of the ground. In sites that contained very dense, uniformly distributed browse species (i.e., grassland sites with uniform low-growing rose and leadplant patches) we used a 6.25 m^2 sampling area. At all other sites we used 25 m^2. We alternated the position of the browse plot each field season (see above), so overlap did not occur among field seasons. We separated leaves and twigs for weighing. We dried browse biomass in an oven at 90°Celsius for 48 hours and recorded the weight to the nearest 0.1 g. We used a double-sampling procedure to improve sampling efficiency of shrub production. In 2005, 2006 and 2008 a percent coverage ocular estimate of each browse species was made before the plot was clipped. Although we used the larger sampling plot specifically for shrub production, we also clipped any shrub or woody species present in the smaller herbaceous plot.

Data analysis

Double sampling. In 2005, every site was clipped and weighed and we used range-site specific regression equations to evaluate the relationship between standing herbaceous biomass and visual obstruction readings. We used linear regression (R 2.6.0; R Development Core Team 2007) to relate visual obstruction readings to total standing biomass. We used residual plots, histograms, and Q-Q plots to assess assumptions of the analysis. For sites that did not have a significant relationship between visual obstruction and biomass, we used the clipping and weighing technique exclusively. For sites where the relationship was significant between visual obstruction and biomass, some production estimates were predicted with the double-sampling technique. We continued to measure visual obstruction and ocular coverage of all sites before clipping, regardless of the significance of the method to that specific range or woodland site. The regression equation used to estimate biomass from visual obstruction or ocular coverage included data from each year 2005–2008, it was not based solely on 2005 readings. We evaluated visual obstruction, ocular percent cover and a combination of both readings to predict biomass for each range and woodland site. We evaluated nonlinear transformations of each variable, and used the method with the strongest predictive ability, based on the r^2, to estimate biomass.

We also evaluated double-sampling for shrub production estimates. We used simple linear regression to determine the relationship between ocular coverage and browse biomass. We developed separate regression equations for twig and foliage biomass of each species, and evaluated residual plots, histograms, and Q-Q plots to assess assumptions of the analysis. No browse plots were clipped in 2007 due to a shortage in budget/staff, however browse ocular coverage was recorded to estimate browse biomass in 2007.

Species composition. We calculated the proportion of total biomass attributed to each forage species per range and woodland site and calculated the yearly production that consisted of cool-season, warm-season, forb and shrub vegetative species and palatable and unpalatable species. Species were considered palatable if they were documented to be consumed by any of the 6 ungulate species in CSP at any time during the year or the plant's development (Larson and Johnson 1999). For range sites, we used contingency tables (Zar 1996) to test whether vegetative composition differed among years and to compare observed with expected NRCS composition. We also compared the observed dominant forage species to the dominant species expected in response to overgrazing (Table 1). We estimated condition for range sites based on NRCS guidelines for proportion of composition consisting of native vegetation, averaged over 4 years of data collection for each range site (2005–2008; Soil Conservation Service 1990). We used Pearson correlations (Zar 1996) to evaluate the relationship between climate variables and the proportion of cool-season, warm-season, forb and shrub species that constituted total biomass for each year.

Building the forage production model. We used a repeated-measures linear mixed model (PROC MIXED; SAS institute 2001; Littell et al. 1998) to predict herbaceous forage production throughout CSP. Total weight was the response variable and we evaluated 18 explanatory variables (Table 2). We evaluated all explanatory variables as fixed effects and used year as a random effect. We used a variable labeled 'cageID' to identify which plots were repeated samples according to year. We specified the maximum likelihood estimation of fixed effects in PROC MIXED. We determined which covariance structure was appropriate for the model by running the full model with compound symmetry, autoregressive, and unstructured covariance structures and chose the covariance structure in the model with the lowest Akaike's Information Criterion (AIC).

We used a 2 step process to build a predictive model for forage production: 1) we first evaluated the proper form of variables (linear, pseudothreshold or quadratic) for each individual parameter in a model with only intercept and proceeded with the variable form that resulted in the lowest AIC; 2) we used a manual procedure to add variables to the model. Beginning with the intercept-only model, we tested each variable (the form that passed step 1) using a deviance-ratio test (Williams et al. 2001; $\alpha = 0.05$) to determine if it could be added to model and added the one variable that passed the deviance test and had the lowest AIC score. If a variable was added, we then tested whether all remaining variables could be added to that model one at a time, and added the variable that passed the deviance test with the lowest AIC score. We continued to test whether variables could be added to the model until no variables passed deviance ratio tests against the previous model. We then tested biologically-relevant interactions between the main-effects variables in the final model, and added any interactions using the same process as above. We did not fit *a priori* models because we were less interested in assessing support among candidate models than in developing a predictive model.

Spatial model of forage production. We used the final herbaceous production model, hereafter the empirical model, to predict forage production in CSP at each 30 × 30 m cell grid in ArcGIS 9.0. Because some climatic variables entered into the empirical model, the final spatial model was not static, and forage production changed among years.

We used information on the percent of biomass of each range site that was composed of palatable forbs and palatable grasses, based on Larson and Johnson (1999) and results in Chapter 4, to estimate the amount of biomass in each range site calculated from the final model that was composed of palatable forbs, grasses and sedges. Thus, we excluded those plants that are not likely to be consumed by ungulates from the biomass model. We used the final palatable-adjusted model projected in ArcGIS to compute the total amount of palatable forage produced under average climatic conditions, in a spatially-explicit manner.

Evaluating the forage production model. We used 10-fold cross validation (Kohavi 1995) to evaluate our final forage production model. We divided our data into 10 subsets, each containing training and testing groups. We used Huberty's (1994) rule-of-thumb to compute a training-to-testing ratio of 0.8:0.2. We used stratified random sampling to select sampling sites for placement in the testing group, to ensure that range and woodland site were equally represented, which reduces both bias and variance (Kohavi 1995), and removed all repeated measures of any site that was selected for the testing dataset. For each fold of the cross validation, we used the training dataset to build a predictive model, and compared predicted values to the observed values in the testing dataset. We calculated the mean bias error (MBE) and root mean square error (RMSE) between the observed and predicted values for each fold in the cross-validation. Mean bias error is an index of the magnitude of the under- or over-prediction of the model and is calculated as

$$MBE = \frac{\sum_{i=1}^{n} \left(p_i - o_i\right)}{n}$$

where p_i is the ith predicted value, o_i is the ith observed value, and n is the number of data pairs. The RMSE is an index of the average deviation between predicted and observed pairs regardless of sign, and is calculated as

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} \left(p_i - o_i\right)^2}{n}}.$$

We averaged MBE and RMSE values across folds for each range and woodland site, to evaluate model performance of each site, as well as across range and woodland sites for a total index of model performance.

In addition to cross-validation we partitioned the variation in forage production explained by the final model. Process variation is the variation in forage production among years, and is broken into model variation, the variation that is explained by the model, and the residual variation, or unexplained variation (Franklin et al. 2000). We used the formula:

$$\sigma^2_{\text{process}} = \sigma^2_{\text{model}} + \sigma^2_{\text{residual}}$$

where σ^2 *process* = exp((-2 × the maximized log likelihood of the intercept-only model)/*n*), and σ^2 *residual* = exp((-2 × the maximized log likelihood of the full model)/*n*), to evaluate the predictive ability of each model (Franklin et al. 2000). Using the above formula we can calculate model variation, which is an estimate of the percent variability explained in forage production by the final model.

Comparison to NRCS estimates. We compared our model to a modified NRCS model similar to what is used by CSP managers. This modified NRCS model used the median production value for soil units in average years (Natural Resource Conservation Service 2002). For soils that composed woodland grazable sites, we used a canopy cover layer to break each site into ≤ 25%, 26-50%, and >50% canopy closure, and used the "average" climate year production estimates for each canopy closure and woodland site combination provided by the NRCS. Custer State Park managers assume that production on 'steep warm slope' and 'steep cool slope' are 83% of total production on 'warm slope' and 'cool slope', respectively, and that 'steep rocky side slope' is 63% of total production on ‘rocky side slope’ based on the amount of rock in those soil units. Range condition ratings are used to further modify the production per soil units. Range conditions of excellent, good, fair, or poor are given to each range site based on the proportion of native community that is present compared to non-native forage species (Natural Resource Conservation Service 2002). Multipliers of 1.00, 0.75, 0.50, and 0.25 are applied to range sites in excellent, good, fair, and poor, respectively. These condition ratings are made separately for 3 different “pastures”, areas of the park where fences restrict bison use during parts of the year in CSP (Figure 1). All woodland sites were considered in ‘good’ condition during all years. Finally, a modification based on the two-year weighted moving mean of precipitation is made to all range and woodland sites. This two-year weighted moving mean is calculated as:

$$2\mathrm{yr}\bar{x} = \left[\left(\frac{precip_i}{precip_y}\right) \times 0.75\right] + \left[\left(\frac{precip_j}{precip_y}\right) \times 0.25\right]$$

where $precip_i$ is the total annual water-year precipitation (Oct. 1 – Sep. 30) for the previous (not current) year, $precip_j$ is the total annual water-year precipitation for the year preceding year i, and $precip_y$ is the 25-year mean of total annual water-year precipitation. The ‘$2\mathrm{yr}\bar{x}$’ is multiplied by the biomass calculated from the above process for all range and woodland sites. The result was the estimated biomass production for year $i + 1$. This weighted mean of water-year precipitation was determined to be a good indicator of forage production for CSP by NRCS staff (G. Brundige, CSP, personal communication). This model was slightly different than the one used by CSP managers as they did not have access to the same canopy cover layer that I used.

We used climate variables specific to each year 2005–2008 to predict biomass using both the empirical and the modified NRCS model. We also compared biomass estimates from each model in "normal" climatic conditions, using the 25-year mean for spring precipitation and mean ordinal date of spring frost (2005–2008) for the empirical model, and weighted 2-year moving mean of 1.00 and typical range condition ratings per pasture (G. Brundige, personal communication) for the modified NRCS model. We used the raster calculator in the spatial analyst toolbox in ArcGIS to display the spatially explicit differences in the two models by subtracting the modified NRCS model from the empirical model.

We used the 'difference' raster to test hypotheses about what environmental attributes corresponded to differences between the two models. We used program R (2.6.0; R Development Core Team 2007), and the RUF.FIT package (Marzluff et al. 2004) to test our hypotheses. The RUF.FIT package performs a maximum likelihood equivalent to multiple linear regression while accounting for spatial autocorrelation in the variance estimates. We used RUF.FIT to relate variation in the difference between the two models that can be attributed to variation in environmental attributes. We first calculated the log of the absolute values of the difference between the two models (empirical – NRCS), and then returned the original sign (+ or -) to that value; this was the response variable in our analysis. We evaluated 5 variables (canopy cover, burn, slope, pasture, and elevation) in a model with range and woodland site to test our hypotheses. We ranked models according to AIC scores to determine which models were most important in accounting for differences between our predictive model and the modified NRCS model.

Finally, because the modified NRCS model used by CSP managers is likely different than what other range managers typically use to estimate biomass (i.e., the use of the two year moving mean in place of the favorable, average, and unfavorable climate modifiers), we also compared biomass at sampling sites with unmodified NRCS production estimates. We classified each year 2005–2008 into ‘favorable’, ‘average’, and ‘unfavorable’ categories based on the ratio of the total annual precipitation to the 25-year mean of total annual precipitation. We used typical range conditions per pasture (G. Brundige, CSP, personal communication) for each year. We calculated the MBE and RMSE between observed biomass and the unmodified NRCS and modified NRCS model estimates at each sampling site, and compared these values to the empirical model.

Shrub production per range site. We calculated 95% confidence intervals of mean production of shrub species for each range and woodland site. We also calculated proportion of biomass that consisted of foliage and annual growth of woody twigs for each shrub species. We calculated total shrub production for CSP by multiplying the mean shrub production per 30 m^2 by each range and woodland site raster in GIS, and summing the entire raster. We also calculated total shrub production per range and woodland site and used the upper and lower limits of the confidence intervals to calculate maximum and minimum production per range and woodland site and for the entire study area. We multiplied the mean, maximum and minimum species-specific shrub production for each range and woodland site by the proportion of total weight for each shrub species composed of new woody growth and foliage to determine species-specific foliage and new woody growth biomass.

RESULTS

We clipped 150, 156, 92, and 351 biomass plots in 2005, 2006, 2007 and 2008, respectively. We estimated biomass based on ocular cover or visual obstruction for 19 plots in 2006 and 65 plots in 2007. This resulted in a total of 833 measurements of biomass which we imported into SAS to build our mixed model.

Double sampling

The double-sampling technique varied in effectiveness to estimate biomass among range and woodland sites (Table 3). The visual obstruction technique performed best for the clayey, overflow, savannah, and silty footslope range and woodland sites, whereas the percent ocular coverage performed best for the cool slope and rocky side slope woodland sites, and an equation containing both visual obstruction and ocular percent cover worked best in the shallow ridge, steep rocky side slope, warm slope, and steep warm slope woodland sites. The double sampling technique did not perform well in the shallow, silty, steep cool slope, stony hills, and thin upland range and woodland sites.

Forage species composition

The composition of warm and cool-season, shrub, and forb communities did not match NRCS expected distributions for any of the range sites (χ_2^2 range = 12.2–41.3, $P \leq$ 0.001–0.002; Table 7). All range sites except the silty site had lower than expected composition of warm-season grasses, and all of the range sites except for the savannah range site had higher than expected composition of forbs and shrubs (Table 7). The clayey, savannah, and thin upland range sites were dominated by forage species indicative of the historic climax communities (Table 6). The overflow, silty, and stony hills range sites were dominated by forage species that are indicative of grazing, and the shallow range site was dominated by forage species indicative of prolonged heavy grazing (Table 6).

Most (6 of 7) range sites were dominated by either Kentucky bluegrass or western wheatgrass, and most woodland sites (5 of 8) were dominated by Kentucky bluegrass (Table 4). Dominant forbs included fringed sagewort (*Artemisia frigida*), wild bergamot (*Monarda fistulosa*) and cudweed sagewort (*Artemisia ludoviciana*; Table 4). The amount of biomass composed of palatable species varied among range and woodland grazable sites (Table 5), but range sites consisted of a slightly higher percentage of palatable species ($\bar{x}$ = 96.5, SE = 0.6) than woodland sites ($\bar{x}$ = 91.3, SE = 2.0). The composition of warm-season and cool-season grasses, forbs and shrubs differed by year ($\chi_9^2 = 2370$, $P \leq 0.001$), which was driven by a higher amount of warm-season grasses, and a lower amount of cool-season grasses, forbs and shrubs in 2005 compared to all other years (χ_3^2 range = 13.7–18.4, $P \leq 0.001$–0.003). All other years did not differ from one another (χ_3^2 range = 0.469–0.556, $P = 0.905$–0.926) in vegetative composition. There was no connection between variability in climate across the study period and forage composition based on Pearson correlations.

Forage production model

We converted the forage weight from g/0.25m^2 to kg/ha, and log-transformed the response variable because it was heavily left-skewed. The unstructured covariance structure performed better ($AIC_{wt} = 1.00$) for our data than compound symmetry or autoregressive. The top model to predict forage production included range and woodland site (15 categories), current year spring precipitation, previous year spring precipitation, ordinal day of last spring frost, a pseudo-threshold form of canopy closure, a quadratic form of elevation, a binary (on / off) prairie dog colony variable, and slope (Table 8). All two-way interactions among canopy closure, slope and elevation were evaluated and were not added to the model.

The final model explained 40% of the variability in herbaceous forage production. The model under-predicted biomass by 336 kg/ha on average, across all range and woodland sites, based on the 10-fold cross-validation. The total average deviance (RMSE) between observed and predicted biomass was 1,306 kg/ha across all range and woodland sites, however 8 of the 15 range and woodland sites performed better than the overall average RMSE (Table 9).

We also evaluated the 3 climatic factors, total current-year spring (1 April – 30 June) precipitation, total previous-year spring precipitation, and the date of the last spring frost on forage production with all other variables in the model held constant (Figure 4). Although both current (Figure 4A) and previous (Figure 4B) year spring precipitation have positive effects on forage production, the current year spring precipitation is the most influential climate variable. The date of last spring frost (Figure 4C) was negatively related to forage production, but the relationship was not as strong as either precipitation variable.

The final model based on the 25-year mean (1984-2008) for spring precipitation and the mean date of last spring frost from 2004-2008 predicted that 30,930,793 kg of biomass was produced annually in CSP (Figure 5). Based on the available literature, we suspected that our model was over-predicting biomass in areas of high canopy cover (> 65%; Bennett et al. 1987). Thus, we eliminated biomass under canopy cover greater than

65%. We used this model, modified for biomass under high canopy cover, for further analysis. This adjustment reduced the biomass prediction for an average year to 28,499,217 kg. Adjusting for palatable biomass, 23,712,697 kg of forage would be available for wildlife in a normal year (Figure 6), although CSP managers typically only allocate 25% of total production, thus managers would allocate 5,928,174 kg for wildlife use.

Comparison to NRCS estimates

The modified NRCS model produced estimates similar to the empirical model (Figure 7); the empirical-based forage production model predicted 3,352,021–7,008,114 kg, or 16 to 28%, less than the modified NRCS forage model using climate conditions specific to 2005 and 2006; but predicted 3,302,552–8,119,856 kg, or 15 to 25%, more than the NRCS forage model using climate conditions specific to 2007 and 2008 (Table 8). Using climatic attributes for an "average" year, the empirical model predicted 2,479,189 kg, or 9.5%, more than the modified NRCS model (Table 8). The empirical model predicted higher biomass in all range and woodland sites except for the silty, silty footslope, rocky side slope, steep rocky side slope range and woodland sites and the prairie dog colony for an average year (Table 8). Although biomass production per range and woodland site varied among years for each model, the empirical model consistently predicted higher biomass for the shallow, shallow ridge, steep cool slope, steep warm slope, thin upland, warm slope range and woodland grazable sites, and the modified NRCS model consistently predicted higher biomass on prairie dog areas (Table 8).

The slope model was most supported (Table 11) to explain differences in biomass estimates between the empirical and modified NRCS models (Figure 8). This relationship appeared to be driven by higher biomass predictions in areas of steep slopes with the modified NRCS model, although the empirical model predicted higher biomass in the steep woodland grazable sites. Compared to the observed biomass at each sampling site, the modified NRCS model over-predicted an average of 140 kg/ha biomass at each sampling site and there was a total average deviation between observed biomass and the modified NRCS estimates of 1,282 kg/ha (Table 7). Based on the MBE and RMSE, the modified NRCS model may appear to be better at prediction. However, the range and woodland-site specific MBE and RMSE values show that the empirical-based model is closer to the observed biomass values for almost all range and woodland sites except for the silty footslope and thin upland range and woodland sites (Table 9). Further, the 95% CI for the overall RMSE based on the cross-validation of the empirical model (1,235−1,377 kg/ha) overlaps the overall RMSE for the modified NRCS model.

The unmodified NRCS estimates were the least accurate method to predict forage biomass in CSP. Total annual ‘water-year’ precipitation was 98, 92, 85, and 95% of the 25-year mean for 2005, 2006, 2007 and 2008, respectively. Thus, for the unmodified NRCS production estimates, we used the ‘average’ production values for each soil map unit for 2005, 2006, and 2008, and the ‘unfavorable’ production values for 2007. The unmodified NRCS estimates on average under-predicted biomass at each sampling site by 410 kg/ha (Table 9), and deviated a total of 1,328.4 kg/ha from observed biomass on average. The empirical model performed better for most range and woodland sites compared to the unmodified NRCS estimates with the exception of the overflow, and the silty footslope range and woodland sites.

Shrub production

We believe the forage production model based on herbaceous sampling plots produced a more reasonable estimate of shrub production than our larger shrub sampling plots. Because we also clipped shrub species that were present in the smaller herbaceous plots, we can use the forage production model to estimate biomass of most shrub species. However certain species that never occurred in herbaceous plots such as mountain mahogany, skunkbrush, and beaked hazelnut, can only be estimated from the shrub-sampling plots. Dominant shrubs included ponderosa pine, raspberry (*Rubus ideaus*), western snowberry (*Symphocarpus occidentalis*), and leadplant (*Rhus aromatica*) (Table 12). Biomass production of shrub species was highly variable both within range sites and across years (Table 12). Our shrub sampling technique produced estimates so variable that only 14% of biomass estimates did not contain 0 in the 95% confidence interval. Only 74,194 kg of shrub biomass, 14,080 kg of deciduous foliage, and 60,114 kg of evergreen foliage or new woody twig growth was attributed to mean shrub production on the landscape. Applying the upper and lower limits of the 95% confidence intervals for the means, between 1,842 and 119,796 kg of shrub biomass is produced in CSP in a typical year. Rocky side slope, steep rocky side slope, and steep warm slope comprised 68% of the total shrub production, most of which was attributed to ponderosa pine (Table 12). Using the forage production model, 4,071,643 kg of shrub biomass was estimated to be produced in CSP under normal climate conditions (Table 13).

DISCUSSION

Forage species patterns

The difference between the species composition we observed in CSP and that predicted by NRCS production table estimates has important implications for the use of those tables to predict biomass and carrying capacity. Although managers should integrate range condition scores into biomass production estimates, which accounts for how far the true species composition varies from the native climax or expected NRCS composition, this only decreases the biomass value and may not be an appropriate representation for the community. For example, high amounts of introduced cool-season grasses such as Kentucky bluegrass and timothy (*Phleum pratense*) would decrease range condition scores and thus biomass estimates, even though these are palatable forage species and can be important components of wild and domesticated ungulate diets (Larson and Johnson 1999). There is considerable evidence that biomass does not always correlate with range condition (Cook et al. 1965, Fischer and Turner 1978, Friedel 1981, Frost and Smith 1991). Biomass estimates and species composition published by the NRCS are rarely tested empirically, but have been used to validate and build other biomass models (Epstein et al. 1996, 1997a, and 1997b, Paruelo et al. 1997, Kiniry et al. 2002, Hunt and Miyake 2006) with no field validation. Hunt and Miyake (2006) found differences in stocking rates based on NRCS estimates to those based on remote-sensing techniques, but did not use field data in the comparison. The NRCS does not provide information on the number of years and conditions under which biomass is calibrated on range and woodland grazable sites or soil map units, which means managers should not assume these estimates can be applied to the particular conditions on their management areas. We recommend all NRCS production estimates be validated with field data spanning a variety of climatic conditions.

The forage species composition in CSP indicates that native, warm-season grasses such as bluestems may be decreasing as Kentucky bluegrass, western wheatgrass, sedges and forbs increase in CSP, despite climate conditions that favor warm-season grass production. Spring droughts in the northern mixed-grass prairie typically result a shift from cool-season to warm-season grass production (Heitschmidt et al. 2005). Although spring precipitation was below average in CSP from 2004–2007, cool-season grasses, particularly western wheatgrass and Kentucky bluegrass, dominated most range and woodland sites. Dominance by these cool-season grasses is considered undesirable for some range sites, even though both grasses are utilized by grazing animals (Larson and Johnson 1999). Forb abundance also generally increases with grazing intensity (Patton et al. 2007), and grazing by bison in WICA was documented to increase forb cover (Cid et al. 1991). Managers may consider management actions that increase warm-season production, such as a reduction of stocking rates or spring burning (Herbel and Anderson 1959, Hover and Bragg 1981, Gillen et al. 1987, Vinton et al. 1993) given that many of the range sites were dominated by plant species considered to be indicative of heavy grazing, and forb and shrub cover in many range sites was higher than expected by NRCS estimates.

Forage production model

The importance of slope and elevation on biomass estimates, even after the range and woodland site categorical variable was added to the model, has important implications. The NRCS estimates do not consider variation in slope, elevation, or other topographical features within the range and woodland sites. Even if managers use biomass estimates that are specific to individual soil map units, the slope within certain soil complexes in our study area can vary up to 40% (Soil Conservation Service 1990). There is abundant evidence that slope and elevation can be important to herbage biomass and species composition (Dix 1958, Matthes-Sears et al. 1988, Peterson and Pickett 1990, Raich et al. 1997, Gillen and Sims 2006). Degree of slope affects the plant community by influencing factors such as soil stability and erosion, runoff, and receiving insolation (Brady and Weil 2002), and elevation can influence temperature, atmospheric pressure, and solar radiation (Korner 2007). Our model suggests the variation within these sites due to slope and elevation significantly affect biomass production. Failing to account for such variation when estimating biomass may introduce considerable error into carrying capacity estimates depending upon the topographical variability in an area. To our knowledge, this is the first study to evaluate the importance of slope and elevation in production models containing range and woodland site categorical variables.

Our findings support other research which suggests that precipitation is the prime factor influencing productivity (Biondini et al. 1998, Heitschmidt et al. 1999, Heitschmidt et al. 2005), and that spring precipitation is more important than annual precipitation in northern mixed grass prairie (Andales et al. 2005, Heitschmidt et al. 2005). Previous spring precipitation likely plays an important role in the ability of the vegetation to react to current precipitation (development of root biomass) and in its importance to soil moisture at the beginning of the growing season (Hansen et al. 1982, Lauenroth and Sala 1992), which greatly affects biomass production in the northern mixed-grass prairie (Holderman and Goetz 1981). The amount of cool-season grasses in

CSP likely increases the importance of spring precipitation in our model (Heitschmidt et al. 2005). The only other important climate variable in our model was the date of the last spring frost, which was negatively related to forage production. This is not surprising because spring temperatures regulate the length of the growing season (George et al. 1988), and as the date of last spring frost increases (is later in the season), the probability of having a short spring and less precipitation increases (George et al. 1989).

Given the size and the heterogeneity of range and woodland sites of our study area, the likelihood of explaining a significant amount of variation with our forage production model was low. Although other biomass models have reported higher predictive success and lower error rates (Smoliak 1986, Milchunas et al. 1994, Andeles et al. 2005 and 2006), they are typically based solely on range production and exclude woodland site production, have low variability in range sites (generally < 3 range sites), and low variability in topographic features such as slope and elevation. However, Lauenroth and Sala (1992) modeled forage production in shortgrass prairie with a similar predictive success of 40%. Additionally, many of the soil map units in CSP are classified as complexes, where two range or woodland sites are so closely intertwined on the landscape that it is difficult to separate them when mapping the area (Brady and Weil 2002). Soil complexes could be composed of soils that fell into different range or woodland site categories, and we classified the soil complex into the range or woodland site of the dominant soil in the complex. Thus, we likely had unaccounted variability within range or woodland sites due to incorrect classification of sites. Another factor that may have reduced our predictive ability is grazing history. Derner and Hart (2007) found that the ability of spring precipitation to predict biomass decreased with moderate to heavy stocking densities. Although we excluded grazing in our sampling plots, the effects of 80+ years of continuous grazing by bison, elk and other wildlife likely impacted our ability to predict forage production. Despite the relatively low amount of the variability explained by the empirical model, the model performed better at estimating biomass at most range and woodland sites when compared to NRCS estimates based on production tables.

Comparison to NRCS estimates

There are several reasons why our empirical model generally predicted higher biomass than the modified NRCS model. First, the modified NRCS model predicted forage production under 3 broad canopy cover categories (0-25%, 25-50% and > 50%) while our model used a continuous multiplier of canopy cover to modify production. This continuous multiplier allowed higher production estimates in the lower end of each range than would be allowed with the modified NRCS model, and in general allows more precise estimates of production. Second, the assumptions of production on steep woodland sites used by CSP managers, which NRCS does not include, were lower than what we estimated with our empirical data. These assumptions were based on the amount of rock in the soil types that composed each woodland site. Third, the modified NRCS model uses real-time field measurements of range condition to estimate biomass. These estimates of range condition are based on the species composition of the vegetative community, and eliminate unpalatable species from the biomass estimate. The empirical model estimates total biomass, including unpalatable species unlikely to be consumed by wildlife, which is then linked to species-specific production tables, thus we would expect biomass predictions to be higher with the empirical model.

Our comparison shows that while the empirical model is more effective at predicting biomass, the unmodified NRCS estimates would not result in a drastic overstocking of the rangeland. The unmodified NRCS estimates performed the poorest compared to the empirical and modified NRCS models, although it tended to underestimate forage production while the modified NRCS model tended to overestimate forage production. It is likely that most range managers would use unmodified NRCS estimates, rather than the modified NRCS model that CSP managers use. It is very important that range managers validate these NRCS production estimates for their specific management areas given the poor performance of the unmodified NRCS estimates, which although in our case underestimated forage production, may overestimate production elsewhere.

Shrub production

Our estimates of shrub production yielded very wide confidence intervals, suggesting that the combination of heterogenous growth forms of shrub and seedling species vs. low homogenous and sod forming grass species and our sampling approach made it difficult to estimate shrub production with high precision. Similarly, Uresk and Severson (1989) also reported low predictive ability for shrub production models for the Black Hills. Given the importance of shrub species to wildlife diets, especially during winter (Chapter 4), we recommend further monitoring and validation of shrub production estimates. However, the shrub production estimates calculated with the empirical forage production model may be used in place of those we calculated using the larger shrub sampling plots. These are much higher estimates of biomass, and appear to be more reasonable than our other estimates.

MANAGEMENT IMPLICATIONS

Stocking-rate decisions are critical to the long-range stability of range ecosystems and depend on accurate estimates of forage production, which can be aided by decision support tools including forage production models. Decision-support tools can be especially important to land management in the northern Great Plains, where variability in climate (precipitation and temperature) is highly influential to biomass production (Knapp and Smith 2001). Variation in biomass does exist within range and woodland sites due to topographical variation in slope and elevation that is not accounted for in NRCS estimates. Thus, in areas of high topographic variation, the difference between actual and NRCS-based estimates of biomass production has the potential to be greater than uniform areas of flat topography. However, unmodified NRCS estimates did not over-estimate carrying capacity on the rangeland in CSP. It is nonetheless important for managers to validate NRCS production estimates, range condition, and the response of biomass to variation in climate and grazing for their particular study areas. We were surprised that NRCS estimates were rarely validated in the literature, and often assumed to represent true biomass production.

In CSP, there were advantages to both the empirical and NRCS-based forage production models. The empirical model requires less labor, and thus funding, to implement and needs only 3 simple climatic inputs, whereas the modified NRCS model requires field-based measurements of range condition. However, because the modified NRCS model requires field measurements, it may better reflect biomass production in certain years, especially in climatic conditions outside of the range that we observed. However, spring precipitation totals ranged from 67 to 129% of normal during our study period, indicating a good range of conditions. Furthermore, range condition scores do not always correlate with biomass production, especially in rangelands where Kentucky bluegrass and other non-native, but palatable, grasses are present. When compared to observed biomass, both models performed better in certain range and woodland sites, although the empirical model generally performed better than the modified NRCS model. We recommend CSP managers utilize both models to estimate biomass and aid in management decisions. We think the modified NRCS model likely gives a better estimate of production within the deferred grazing pastures, as we did not sample separately within pastures to create the empirical model. We recommend the modified NRCS model be used to estimate production in the silty footslope, stony hills, and thin upland range and woodland sites, and the empirical model be used to estimate forage production in all other range and woodland sites. It is likely most beneficial to estimate biomass using both models and use the most conservative estimate of biomass production for management purposes, or to use the range of the two estimates. The empirical model is most useful for determining ungulate carrying capacity since it produced species-specific biomass estimates; especially considering the species composition in CSP appears to differ from those assumed by NRCS production tables.

LITERATURE CITED

Andales, A. A., J. D. Derner, P. N. Bartling, L. R. Ahuja, G. H. Dunn, R. H. Hart, and J. D. Hansen. 2005. Evaluation of GPFARM for simulation of forage production and cow-calf weights. Rangeland Ecology and Management 58:77–88.

Andales, A. A., J. D. Derner, L. R. Ahuja, and R. H. Hart. 2006. Strategic and tactical prediction of forage production in mixed grass prairie. Rangeland Ecology and Management 59:576–584.

Benkobi, L., D. W. Uresk, G. Schenbeck, and R. M. King. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. Journal of Range Management 53:627–633.

Bennett, D. L., G. D. Lemme, and P. D. Evenson. 1987. Understory herbage production of major soils within the Black Hills of South Dakota. Journal of Range Management 40:166–170.

Beyer, H. L. 2004. Hawth’s Analysis Tools for ArcGIS. Available at http://www.spatialecology.com

Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie. Ecological Applications 8:469–479.

Brady, N. C., and R. R. Weil. 2002. The nature and properties of soils. Thirteenth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. Journal of Range Management 44:100–105.

Cook, C., K. T. Wayne, and L. E. Harris. 1965. Effect of range condition and utilization on nutritive intake of sheep on summer ranges. Journal of Range Management 18:69–73.

CSP. 1995. Custer State Park Resource Management Plan 1995–2010. Unpublished document.

Derner, J. D., and R. H. Hart. 2007. Grazing-induced modifications to peak standing crop in northern mixed-grass prairie. Rangeland Ecology and Management 60:270–276.

Dix, R. L. 1958. Some slope-plant relationships in the grasslands of the Little Missouri Badlands of North Dakota. Journal of Range Management 11:88–92.

Dodd, J. L., W. K. Lauenroth, and R. K. Heitschmidt. 1982. Effects of controlled SO_2 exposure on net primary production and plant biomass dynamics. Journal of Range Management 55:572–579.

Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1996. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. Journal of Vegetation Science 7:777–788.

Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1997a. Productivity patterns of C_3 and C_4 functional types in the U.S. Great Plains. Ecology 78:722–731.

Epstein, H. E., W. K. Lauenroth, and I. C. Burke. 1997b. Effects of temperature and soil texture on ANPP in the U. S. Great Plains. Ecology 78:2628–2631.

Fischer, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semiarid zones. Annual Review of Plant Physiology 29:277–317.

Franklin, A. B., D. A. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Friedel, M. H. 1981. Studies of central Australian semidesert rangelands. I. range condition and the biomass dynamics of the herbage layer and litter. Australian Journal of Botany 29:219–231.

Frost, W. E., and E. L. Smith. 1991. Biomass productivity and range condition on range sites in southern Arizona. Journal of Range Management 44:64–67.

George, M. R., C. A. Raguse, W. J. Clawson, C. B. Wilson, R. L. Willoughby, N. K. McDougald, D. A. Duncan, and A. H. Murphy. 1988. Correlation of degree-days with annual herbage yields and livestock gains. Journal of Range Management 41:193–197.

George, M. R., W. A. Williams, N. K. McDougald, W. J. Clawson, and A. H. Murphy. 1989. Predicting peak standing crop on annual range using weather variables. Journal of Range Management 42:508–513.

Gillen, R. L., and P. L. Sims. 2006. Stocking rate and weather impacts on sand sagebrush and grasses: a 20-year record. Rangeland Ecology and Management 59:145–152.

Gillen, R. L., D. Rollins, and J. F. Stritzke. 1987. Atrazine, spring burning, and nitrogen for improvement of tallgrass prairie. Journal of Range Management 40:444–447.

Heitschmidt, R. K., E. E. Grings, M. R. Haferkamp, and M. G. Karl. 1995. Herbage dynamics on 2 Northern Great Plains range sites. Journal of Range Management 48:211–217.

Heitschmidt, R. K., M. R. Haferkamp, M. G. Karl, and A. L. Hild. 1999. Drought and grazing: I. Effects on quantity of forage produced. Journal of Range Management 52:440–446.

Heitschmidt, R. K., K. D. Klement, and M. R. Haferkamp. 2005. Interactive effects of drought and grazing on northern Great Plains rangelands. Rangeland Ecology and Management 58:11–19.

Herbel, C. H., and K. L. Anderson. 1959. Response of true prairie vegetation on major Flint Hills range sites to grazing treatment. Ecological Monographs 29:171–186.

Higgins, K. F., J. L. Oldemeyer, K. J. Jenkins, G. K. Clambey, and R. F. Harlow. 1994. Vegetation sampling and measurement. Pages 567–606 *in* T. A. Bookhout, editor, Research and management techniques for wildlife and habitats. Allen Press, Lawrence, Kansas, USA.

Holderman, C. A., and H. Goetz. 1981. Response of western North Dakota mixed prairie to intensive clipping and five stages of development. Journal of Range Management 34:188–193.

Hover, E. L., and T. B. Bragg. 1981. Effect of season of burning and mowing on an eastern Nebraska Stipa-Andropogon prairie. American Midland Naturalist 105:13–18.

Howe, J. 1994. Managing species diversity on a tallgrass prairie: Assumptions and implications. Conservation Biology 8:691–704.

Huberty, C. J. 1994. Applied Discriminant Analysis. Wiley Interscience, New York, New York, USA.

Hunt, E. R., and B. A. Miyake. 2006. Comparison of stocking rates from remote sensing and geospatial data. Rangeland Ecology and Management 59:11–18.

Jama, A., R. Kaitho, J. Wu, and L. Macopiyo. 2006. A new toolkit for monitoring and forecasting forage supply in the grazing lands of eastern Africa. Pages 349–358 *in* Proceedings of the International Scientific Conference on Desertificiation and Drylands Research. Tunis, Tunisia, Africa.

Kiniry, J. R., H. Sanchez, J. Greenwade, E. Seidensticker, J. R. Bell, F. Pringle, G. Peacock, and J. Rives. 2002. Simulating grass productivity on diverse range sites in Texas. Journal of Soil and Water Conservation 57:144–150.

Kohavi, R. 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection. Pages 1137–1143 *In* Proceedings of the 14th International Joint Conference on Artificial Intelligence. Montreal, Canada.

Korner, C. 2007. The use of ‘altitude’ in ecological research. Trends in Ecology and Evolution 22:569–574.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484.

Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota Agricultural Experiment Station, Brookings, South Dakota, USA.

Lauenroth, W. K., and W. C. Whitman. 1977. Dynamics of dry matter production in a mixed-grass prairie in western North Dakota. Oecologica 27:339–351.

Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397–403.

Littell, R. C., P. R. Henry and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. Journal of Animal Science 76:1216–1231.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411–1427.

Matthes-Sears, U., W. C. Matthes-Sears, S. J. Hastings, and W. C. Oechel. 1988. The effects of topography and nutrient status on the biomass, vegetative characteristics, and gas exchange of two deciduous shrubs on an arctic tundra slope. Arctic and Alpine Research 20:342–351.

Milchunas, D. G., J. R. Forwood, and W. K. Lauenroth. 1994. Productivity of long-term grazing treatments in response to seasonal precipitation. Journal of Range Management 47:133–139.

Mirik, M., J. E. Norland, R. L. Crabtree, and M. E. Biodini. 2006. Hyperspectral one-meter-resolution remote sensing in Yellow National Park: II. Biomass. Rangeland Ecology and Management 58:459–465.

Moore, M. M., and D. A. Deiter. 1992. Stand density index as a predictor of forage production in Northern Arizona pine forests. Journal of Range Management 45:267–271.

Natural Resource Conservation Service, 2002. South Dakota Technical Guide. Available online http://efotg.nrcs.usda.gov

Olenicki, T. J., and L. R. Irby. 2005. Determining forage availability and use patterns for bison in the Hayden Valley of Yellowstone National Park. Final Report to the National Park Service.

Patton, B. D., X. Dong, P. E. Nyren, and A. Nyren. 2007. Effects of grazing intensity, precipitation, and temperature on forage production. Rangeland Ecology and Management 60:656–665.

Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, and I. C. Burke. 1997. ANPP estimates from NDVI for the central grassland region of the United States. Ecology 78:953–958.

Peterson, C. J., and S. T. Pickett. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. Journal of Vegetation Science 1:657–662.

R Development Core Team. 2007. R: A langurage and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raich, J. W., A. E. Russell, and P. M. Vitousek. 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawaii. Ecology 78:707–721.

Ratti, J. T., and E. O. Garton. 1994. Research and experimental design. Pages 1–23 *in* T. A. Bookhout, editor, Research and management techniques for wildlife and habitats. Allen Press, Lawrence, Kansas, USA.

SAS Institute. 2001. Version 8. SAS Institution, Inc. Cary, North Carolina, USA.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. Journal of Ecology 66:573–597.

Smoliak, S. 1986. Influence of climatic conditions on production of *Stipa-Bouteloua* prairie over a 50-year period. Journal of Range Management 39:100–103.

Soil Conservation Service, 1990. Soil Survey of Custer and Pennington Counties, Black Hills Parts, South Dakota. United States Department of Agriculture.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

Uresk, D. W., and K. E. Severson. 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. Journal of Range Management 42:203–208.

Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist 129:10–18.

Wight, J. R., and R. J. Hanks. 1981. A water-balance, climate model for range forage production. Journal of Range Management 34:307–311.

Wight, J. R., C. L. Hanson, and D. Whitmer. 1984. Using weather records with a forage production model to forecast range forage production. Journal of Range Management 37:3–6.

Wight, J. R., and J. W. Skiles, editors. 1987. SPUR: Simulation of production and utilization of rangelands. Documentation and user guide. USDA-ARS, ARS 63. National Technical Information Service, Springfield, Virginia, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Chapter 4. Estimation and hypothesis testing. Pages 33–58 *in*, B. K. Williams, J. D. Nichols, and M. J.

Conroy, editors. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Woods, R., D. R. Betters, and E. W. Mogren. 1982. Understory herbage production as a function of Rocky Mountain Aspen stand density. Journal of Range Management 35:380–381.

Wylie, B. K., D. D. DeJong, L. L. Tieszen, and M. E. Biodini. 1996. Grassland canopy parameters and their relationships to remotely sensed vegetation indices in the Nebraska Sand Hills. Geocarto International 11:39–52.

Xie, Y., Z. Sha, M. Yu, Y. Bai, and L. Zhang. 2009. A comparison of two models with Landsat data for estimating above ground grassland biomass in Inner Mongolia, China. Ecological Modeling 220:1810–1818.

Zar, J. H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, USA.

.

Table 1. Expected dominant forage species, and forage species that increase due to continued heavy grazing, according to the Natural Resource Conservation Service, for each range site in Custer State Park, South Dakota.

Range site	Expected dominant species	Dominant species indicative of overgrazing
Clayey	Western wheatgrass, green needlegrass	Blue grama, buffalograss
Overflow	Big bluestem, other warm-season grasses	Western wheatgrass, Kentucky bluegrass
Savannah	Little bluestem, big bluestem, leadplant	Sedges, yucca, prickley pear cactus
Shallow	Little bluestem, big bluestem	Needleandthread, sideoats grama; continued overgrazing causes needleandthread and sideoats grama to be replaced by sedges, blue grama and weedy forbs
Silty	Big bluestem, little bluestem, western wheatgrass, green needlegrass, needleandthread	Blue grama, Kentucky bluegrass, sedges

Table 1. Continued.

Range site	Expected dominant species	Dominant species indicative of overgrazing
Stony hills	Big bluestem, little bluestem	Western wheatgrass, Kentucky bluegrass; continued overgrazing causes western wheatgrass and Kentucky bluegrass to be replaced by sedges, forbs and weedy grasses
Thin upland	Little bluestem, sideoats grama, green needlegrass, western wheatgrass	Sedges and blue grama

Table 2. Variables evaluated in forage production models for Custer State Park, SD.

Variable	Measurement	Source
Total annual precipitation	Inches	CSP weather station
Moving mean of precipitation	(0.75 × current year precipitation) + (0.25 × previous year precipitation)	CSP weather station
Total spring precipitation	Inches	CSP weather station
Previous spring precipitation	Inches	CSP weather station
Date of last spring frost	Ordinal date	NOAA weather station, Custer, SD
Range or woodland site	15 categories	NRCS soil survey
Canopy closure	%	Spherical densitometer
Slope	%	Clinometer
Terrain ruggedness	Surface ratio	DEM
Elevation	Meters	DEM
Distance to water	Meters	CSP GIS data
Water holding capacity	Inches	NRCS soil survey
Landform	14 categories	NRCS soil survey
Position	4 categories	NRCS soil survey
Prairie dog colony	Binary on / off	CSP GIS data
Aspect	N, S, E, W or none	DEM
Fire-killed forest	Binary on / off	CSP GIS data
Study area	Wind Cave NP or CSP	CSP GIS data

Table 3. Most supported double-sampling equations, based on r^2 and the visual obstruction or ocular coverage techniques, for each range and woodland site in Custer State Park, South Dakota.

Range or woodland site	Method	Equation	r^2 (adjusted)
Clayey	Visual obstruction	biomass(g) = 17.99 + 3.33(robel)[a]	0.683
Cool slope	Ocular coverage	biomass(g) = 1.44 + 65.02(covered)[b]	0.433
Overflow	Visual obstruction	biomass(g) = 17.77 + 2.66(robel)	0.540
Rocky side slope	Ocular coverage	biomass(g) = 33.66 + 20.17(lncovered)[c]	0.410
Savannah	Visual obstruction	biomass(g) = 14.18 + 3.00(robel)	0.504
Shallow	Visual obstruction	biomass(g) = 14.85 + 13.40(lnrobel)[d]	0.166
Shallow ridge	Visual obstruction and ocular coverage	biomass(g) = 20.31 - 0.13(robel) + 11.23(lncovered) + 4.03(robel×lncovered)	0.566
Silty	Visual obstruction and ocular coverage	biomass(g) = -143.84 + 107.20(lnrobel) + 211.64(covered) - 98.41(lnrobel×covered)	0.343
Silty footslope	Visual obstruction	biomass(g) = 10.38 + 1.69(robel)	0.419

[a] robel = average of 4 readings of Robel visual obstruction pole taken on site, [b] covered = ocular estimate of porportion total cover (versus bare ground) of site, [c] lncovered = log of porportion cover estimate, [d] lnrobel = log of Robel visual obstruction value

Table 3. Continued.

Range or woodland site	Method	Equation	r^2 (adjusted)
Steep cool slope	Visual obstruction and ocular coverage	biomass(g) = 17.74 - 78.57(lnrobel) - 98.37(lncovered) + 90.57(lnrobel×lncovered)	0.255
Steep rocky side slope	Visual obstruction and ocular coverage	biomass(g) = -7.58 + 0.68(robel) + 61.50(covered)	0.562
Stony hills	Visual obstruction and ocular coverage	biomass(g) = 10.56 + 25.43(lnrobel) - 10.05(lncovered) + 17.98(lnrobel×lncovered)	0.405
Steep warm slope	Visual obstruction and ocular coverage	biomass(g) = 354.14 - 9.99(robel) + 273.70(lncovered)	0.402
Thin upland	Visual obstruction	biomass(g) = 15.03 + 12.33(lnrobel)	0.328
Warm slope	Visual obstruction and ocular coverage	biomass(g) = 7.71 + 1.37(robel) - 19.07(covered) + 2.96(robel×covered)	0.795

Table 4. Mean proportion and standard error (in parantheses) of biomass constituted by each plant species for each range and woodland site in Custer State Park, South Dakota, 2005–2008.

Range or Woodland Site	*Ambrosia psilostachya*	*Amorpha canescens*	*Andropogon gerardii*	*Antennaria spp.*
Clayey	0.802 (0.398)	0.044 (0.042)	2.381 (1.850)	--
Cool Slope	0.009 (0.009)	--	0.850 (0.842)	--
Overflow	0.179 (0.126)	--	4.093 (2.882)	0.097 (0.096)
Rocky Side Slope	1.644 (1.091)	--	1.492 (0.816)	2.079 (0.814)
Savannah	6.770 (2.851)	1.031 (0.833)	11.383 (4.411)	--
Shallow	3.693 (1.773)	5.261 (2.579)	3.100 (1.683)	--
Shallow Ridge	1.172 (0.627)	--	7.206 (2.754)	--
Silty	3.993 (1.773)	0.777 (0.645)	1.547 (0.603)	1.091 (1.002)
Silty Footslope	--	--	--	2.526 (2.032)
Steep Cool Slope	0.453 (0.453)	1.211 (0.825)	5.03 (2.633)	--
Steep Rocky Side Slope	0.672 (0.672)	0.914 (0.650)	1.110 (0.717)	2.163 (1.409)
Steep Warm Slope	--	--	0.980 (0.679)	--
Stony Hills	1.978 (0.736)	5.937 (1.601)	4.220 (1.219)	0.075 (0.050)
Thin Upland	3.292 (1.803)	0.494 (0.494)	7.060 (2.483)	--
Warm Slope	0.213 (0.119)	0.086 (0.086)	2.662 (0.956)	0.022 (0.022)
Prairie Dog Colony	--	--	9.438 (4.553)	--

Table 4. Continued.

Range or Woodland Site	*Arctostaphylos rubra*	*Artemisia frigida*	*Artemisia ludoviciana*	*Aster spp.*
Clayey	--	0.670 (0.454)	8.413 (2.953)	0.485 (0.421)
Cool Slope	--	--	--	2.88 (1.840)
Overflow	3.694 (2.110)	--	--	--
Rocky Side Slope	3.900 (1.850)	tr[a]	0.932 (0.637)	1.267 (0.841)
Savannah	--	6.473 (2.798)	2.915 (1.619)	0.700 (0.585)
Shallow	--	6.283 (2.629)	2.911 (1.736)	0.344 (0.247)
Shallow Ridge	--	2.118 (1.090)	1.963 (0.992)	0.233 (0.233)
Silty	--	10.226 (3.472)	3.124 (1.537)	0.643 (0.355)
Silty Footslope	0.098 (0.098)	--	--	1.393 (1.171)
Steep Cool Slope	--	0.021 (0.021)	2.994 (2.280)	1.856 (1.178)
Steep Rocky Side Slope	3.403 (1.865)	0.779 (0.571)	tr[a]	2.439 (1.107)
Steep Warm Slope	--	1.714 (1.714)	1.379 (1.268)	0.279 (0.182)
Stony Hills	--	1.175 (0.593)	4.192 (1.201)	0.818 (0.344)
Thin Upland	--	0.170 (0.141)	--	1.513 (1.051)
Warm Slope	--	--	0.139 (0.069)	0.773 (0.428)
Prairie Dog Colony	--	29.565 (7.219)	6.253 (2.135)	0.475 (0.400)

Table 4. Continued.

Range or Woodland Site	*Astragalus spp.*	*Bouteloua curtipendula*	*Bouteloua dactyloides*	*Bouteloua gracilis*
Clayey	--	0.101 (0.097)	1.417 (0.826)	11.803 (3.746)
Cool Slope	--	2.789 (2.227)	--	0.021 (0.021)
Overflow	0.268 (0.165)	--	--	--
Rocky Side Slope	0.168 (0.106)	0.767 (0.614)	--	1.530 (0.842)
Savannah	--	1.108 (0.668)	2.746 (2.739)	22.526 (4.889)
Shallow	0.127 (0.127)	0.812 (0.444)	1.528 (1.273)	8.281 (3.149)
Shallow Ridge	--	2.937 (1.386)	2.117 (1.919)	9.310 (2.694)
Silty	0.017 (0.016)	1.936 (1.367)	0.498 (0.391)	16.898 (3.866)
Silty Footslope	0.243 (0.143)	0.026 (0.026)	0.562 (0.562)	5.872 (3.927)
Steep Cool Slope	0.154 (0.154)	14.009 (4.265)	--	1.938 (1.619)
Steep Rocky Side Slope	0.174 (0.162)	2.787 (1.828)	0.262 (0.262)	0.512 (0.417)
Steep Warm Slope	--	7.417 (3.913)	--	2.120 (0.971)
Stony Hills	0.330 (0.286)	2.615 (0.829)	1.065 (0.748)	8.727 (1.589)
Thin Upland	0.930 (0.667)	1.794 (0.909)	7.225 (5.001)	0.074 (0.056)
Warm Slope	0.038 (0.038)	7.918 (2.668)	0.604 (0.604)	1.432 (0.648)
Prairie Dog Colony	0.099 (0.095)	0.001 (0.001)	--	4.892 (1.849)

Table 4. Continued.

Range or Woodland Site	*Bromus inermis*	*Bromus tectorum*	*Carex spp.*	*Calamovilfa longifolia*
Clayey	4.290 (1.986)	1.452 (0.747)	2.578 (1.170)	1.656 (1.302)
Cool Slope	2.213 (2.090)	0.053 (0.053)	2.986 (1.656)	--
Overflow	9.995 (4.092)	3.006 (2.370)	7.763 (2.909)	--
Rocky Side Slope	0.133 (0.131)	1.820 (1.366)	10.522 (1.751)	0.184 (0.186)
Savannah	--	0.654 (0.446)	7.965 (4.391)	0.846 (0.727)
Shallow	1.400 (1.063)	0.772 (0.767)	6.194 (3.486)	1.093 (0.769)
Shallow Ridge	0.444 (0.444)	0.419 (0.243)	10.048 (3.460)	1.350 (0.881)
Silty	2.018 (2.005)	2.959 (2.941)	1.278 (0.382)	1.379 (0.816)
Silty Footslope	8.174 (3.118)	2.815 (2.815)	9.952 (2.949)	4.963 (3.468)
Steep Cool Slope	--	0.764 (0.686)	2.752 (0.832)	0.306 (0.306)
Steep Rocky Side Slope	3.573 (1.869)	0.038 (0.025)	10.724 (2.663)	--
Steep Warm Slope	--	2.736 (2.467)	0.141 (0.139)	0.394 (0.394)
Stony Hills	3.062 (1.370)	2.227 (1.003)	3.979 (0.622)	0.328 (0.173)
Thin Upland	0.146 (0.146)	3.710 (3.710)	2.894 (1.810)	5.470 (4.113)
Warm Slope	1.249 (0.960)	1.549 (1.311)	14.591 (3.742)	0.620 (0.620)
Prairie Dog Colony	0.463 (0.446)	--	3.453 (1.086)	0.001 (0.001)

Table 4. Continued.

Range or Woodland Site	*Campanula rotundifolia*	*Cirsium arvense*	*Danthonia spicata*	*Dalea purpurea*
Clayey	--	--	--	--
Cool Slope	1.091 (0.870)	0.642 (0.372)	1.190 (0.549)	--
Overflow	0.105 (0.101)	1.137 (0.627)	0.019 (0.019)	--
Rocky Side Slope	0.796 (0.396)	0.335 (0.213)	12.000 (2.584)	0.146 (0.148)
Savannah	--	--	1.435 (1.422)	--
Shallow	0.024 (0.024)	--	0.055 (0.055)	--
Shallow Ridge	--	1.530 (0.874)	2.727 (2.619)	0.711 (0.666)
Silty	tr	--	0.154 (0.154)	0.001 (0.001)
Silty Footslope	0.229 (0.110)	0.006 (0.006)	14.860 (4.571)	--
Steep Cool Slope	1.053 (0.890)	6.720 (2.253)	0.256 (0.213)	--
Steep Rocky Side Slope	2.440 (1.170)	0.505 (0.227)	12.736 (3.057)	0.041 (0.041)
Steep Warm Slope	--	0.131 (0.049)	0.799 (0.734)	--
Stony Hills	0.089 (0.069)	0.062 (0.062)	1.213 (0.767)	0.202 (0.172)
Thin Upland	0.002 (0.002)	--	2.504 (2.346)	0.913 (0.913)
Warm Slope	0.557 (0.332)	0.677 (0.677)	0.464 (0.251)	tr
Prairie Dog Colony	--	0.098 (0.080)	--	--

Table 4. Continued.

Range or Woodland Site	*Dichanthelium oligosanthes*	*Echinacea pallida*	*Elymus elymoides*	*Erigeron spp.*
Clayey	0.053 (0.050)	0.049 (0.047)	0.587 (0.488)	--
Cool Slope	--	--	0.014 (0.014)	--
Overflow	--	--	0.143 (0.142)	0.038 (0.038)
Rocky Side Slope	0.304 (0.167)	--	0.269 (0.266)	0.037 (0.037)
Savannah	0.226 (0.190)	0.215 (0.215)	--	--
Shallow	0.703 (0.695)	0.082 (0.061)	0.777 (0.562)	0.064 (0.064)
Shallow Ridge	1.492 (1.024)	0.124 (0.090)	0.121 (0.121)	0.075 (0.075)
Silty	0.006 (0.006)	0.794 (0.600)	0.172 (0.157)	0.064 (0.053)
Silty Footslope	0.003 (0.003)	--	2.346 (2.346)	0.482 (0.416)
Steep Cool Slope	0.021 (0.021)	0.062 (0.062)	1.760 (1.345)	0.040 (0.040)
Steep Rocky Side Slope	1.044 (0.965)	--	0.078 (0.078)	1.437 (0.772)
Steep Warm Slope	0.046 (0.046)	0.176 (0.155)	0.001 (0.001)	--
Stony Hills	0.186 (0.100)	0.381 (0.239)	0.457 (0.358)	--
Thin Upland	0.036 (0.035)	0.002 (0.002)	--	--
Warm Slope	0.036 (0.030)	--	--	0.070 (0.070)
Prairie Dog Colony	0.258 (0.238)	0.054 (0.050)	0.149 (0.142)	--

Table 4, Continued.

Range or Woodland Site	*Galium boreale*	*Hesperostipa comata*	*Melilotus officinalis*	*Monarda fistulosa*
Clayey	--	1.012 (0.968)	0.208 (0.132)	--
Cool Slope	--	9.673 (4.056)	2.410 (1.502)	4.940 (2.890)
Overflow	0.176 (0.108)	0.169 (0.167)	0.106 (0.095)	1.185 (0.733)
Rocky Side Slope	0.026 (0.019)	0.943 (0.544)	0.051 (0.046)	1.670 (0.684)
Savannah	--	--	--	--
Shallow	--	1.772 (0.791)	0.290 (0.241)	--
Shallow Ridge	tr	6.295 (3.010)	--	--
Silty	0.004 (0.004)	1.257 (0.610)	tr	--
Silty Footslope	0.430 (0.352)	--	0.102 (0.100)	0.927 (0.774)
Steep Cool Slope	--	3.515 (2.173)	1.642 (0.737)	1.279 (0.928)
Steep Rocky Side Slope	0.097 (0.096)	--	2.058 (1.051)	0.875 (0.747)
Steep Warm Slope	2.771 (2.770)	--	0.073 (0.073)	0.664 (0.510)
Stony Hills	0.177 (0.138)	0.931 (0.375)	--	1.231 (0.796)
Thin Upland	--	0.724 (0.529)	--	4.600 (3.518)
Warm Slope	0.106 (0.095)	3.000 (1.418)	--	1.241 (1.044)
Prairie Dog Colony	0.001 (0.001)	0.389 (0.261)	0.598 (0.576)	0.072 (0.069)

Table 4, Continued.

Range or Woodland Site	*Muhlenbergia ramulosa*	*Nassella viridula*	*Pascopyrum smithii*	*Pinus ponderosa*
Clayey	--	1.140 (0.839)	26.448 (4.980)	--
Cool Slope	--	0.300 (0.224)	2.566 (1.086)	--
Overflow	--	1.136 (1.126)	7.674 (4.111)	1.541 (1.227)
Rocky Side Slope	1.984 (1.340)	0.792 (0.441)	5.103 (1.631)	1.998 (1.426)
Savannah	--	--	2.881 (1.683)	3.598 (3.589)
Shallow	--	0.275 (0.209)	11.175 (3.655)	3.475 (2.873)
Shallow Ridge	5.403 (3.031)	0.900 (0.900)	6.005 (2.494)	--
Silty	0.027 (0.027)	0.196 (0.142)	11.468 (3.466)	0.965 (0.853)
Silty Footslope	2.183 (1.984)	0.322 (0.322)	2.813 (2.013)	10.516 (4.661)
Steep Cool Slope	12.196 (4.479)	1.850 (1.652)	3.701 (0.849)	--
Steep Rocky Side Slope	2.223 (0.967)	--	0.942 (0.452)	4.100 (2.058)
Steep Warm Slope	--	0.341 (0.341)	5.211 (2.791)	3.100 (2.852)
Stony Hills	0.500 (0.400)	2.500 (0.818)	22.435 (2.930)	tr
Thin Upland	0.132 (0.132)	2.922 (2.267)	4.937 (2.301)	6.095 (3.780)
Warm Slope	1.875 (1.725)	5.100 (1.446)	4.552 (1.308)	1.872 (1.083)
Prairie Dog Colony	--	0.243 (0.234)	13.746 (5.047)	--

Table 4, Continued.

Range or Woodland Site	*Poa pratensis*	*Psoralidium tenuflorum*	*Ratibida columnifera*	*Rosa spp.*
Clayey	16.107 (5.440)	0.068 (0.065)	--	0.192 (0.183)
Cool Slope	30.876 (5.124)	--	--	--
Overflow	34.772 (4.802)	--	--	0.360 (0.215)
Rocky Side Slope	19.401 (3.163)	tr	tr	--
Savannah	5.949 (1.711)	0.010 (0.008)	--	--
Shallow	19.018 (4.585)	0.225 (0.178)	0.002 (0.002)	2.932 (1.563)
Shallow Ridge	10.904 (3.541)	0.185 (0.159)	0.106 (0.086)	--
Silty	10.447 (2.998)	0.144 (0.143)	0.363 (0.363)	6.369 (2.692)
Silty Footslope	13.513 (4.415)	--	--	0.179 (0.101)
Steep Cool Slope	4.861 (1.789)	0.039 (0.037)	0.024 (0.024)	--
Steep Rocky Side Slope	9.087 (2.126)	--	--	0.196 (0.137)
Steep Warm Slope	8.294 (3.065)	0.022 (0.021)	--	--
Stony Hills	13.100 (1.865)	0.370 (0.134)	--	1.898 (0.618)
Thin Upland	20.019 (4.105)	0.745 (0.488)	--	0.135 (0.096)
Warm Slope	24.053 (3.588)	0.213 (0.180)	--	--
Prairie Dog Colony	3.072 (1.879)	0.298 (0.181)	--	0.825 (0.713)

Table 4, Continued.

Range or Woodland Site	*Rubus idaeus*	*Schizachyrium scoparium*	*Solidago spp.*	*Sporobolus heterolepis*
Clayey	--	1.836 (1.597)	0.078 (0.075)	--
Cool Slope	--	1.490 (1.476)	6.693 (2.933)	--
Overflow	0.574 (0.367)	0.307 (0.255)	0.746 (0.623)	--
Rocky Side Slope	1.613 (0.804)	10.412 (2.590)	0.932 (0.403)	--
Savannah	4.568 (3.195)	13.234 (5.000)	0.068 (0.068)	0.373 (0.372)
Shallow	--	9.110 (4.183)	0.208 (0.175)	1.182 (1.182)
Shallow Ridge	1.126 (0.805)	10.529 (3.514)	0.134 (0.120)	--
Silty	--	5.472 (2.847)	0.540 (0.403)	0.168 (0.168)
Silty Footslope	0.171 (0.171)	1.468 (0.922)	2.133 (0.852)	--
Steep Cool Slope	--	4.125 (2.410)	2.898 (1.886)	0.609 (0.609)
Steep Rocky Side Slope	3.742 (1.212)	7.593 (2.936)	2.399 (1.283)	--
Steep Warm Slope	10.141 (4.357)	0.912 (0.858)	10.817 (7.216)	--
Stony Hills	0.458 (0.322)	1.453 (0.553)	0.189 (0.138)	0.065 (0.061)
Thin Upland	--	1.602 (0.968)	0.251 (0.237)	--
Warm Slope	0.127 (0.107)	6.504 (2.109)	0.155 (0.100)	1.078 (1.078)
Prairie Dog Colony	--	9.494 (4.173)	3.814 (1.982)	--

Table 4, Continued.

Range or Woodland Site	*Symphoricapros occidentalis*	*Symphyo-trichum falcatum*	*Toxico-dendron rydbergii*	*Tragopogon dubius*
Clayey	2.740 (1.590)	1.283 (0.656)	--	--
Cool Slope	2.759 (1.291)	1.758 (1.741)	2.479 (1.710)	0.484 (0.430)
Overflow	7.235 (2.771)	--	0.635 (0.421)	--
Rocky Side Slope	1.681 (0.677)	0.406 (0.321)	--	0.459 (0.402)
Savannah	--	--	--	--
Shallow	0.226 (0.226)	0.089 (0.064)	--	--
Shallow Ridge	--	0.021 (0.017)	0.013 (0.012)	0.825 (0.715)
Silty	1.882 (1.075)	0.392 (0.365)	--	--
Silty Footslope	1.182 (0.493)	0.184 (0.184)	--	--
Steep Cool Slope	2.608 (1.430)	0.455 (0.352)	0.573 (0.469)	0.127 (0.127)
Steep Rocky Side Slope	0.715 (0.328)	0.343 (0.246)	1.305 (1.305)	0.104 (0.085)
Steep Warm Slope	3.845 (2.208)	--	2.144 (2.144)	0.049 (0.049)
Stony Hills	3.320 (1.233)	0.612 (0.249)	0.228 (0.228)	0.231 (0.148)
Thin Upland	6.052 (3.050)	0.366 (0.265)	--	0.217 (0.177)
Warm Slope	0.966 (0.508)	2.039 (1.731)	1.221 (0.803)	0.081 (0.081)
Prairie Dog Colony	0.225 (0.151)	0.214 (0.122)	--	0.071 (0.068)

Table 4, Continued.

Range or Woodland Site	*Trifolium spp.*	Other forb spp.	Other grass spp.
Clayey	0.002 (0.001)	5.308 (2.398)	6.389 (4.481)
Cool Slope	2.792 (2.171)	7.918 (0.926)	7.938 (6.118)
Overflow	0.130 (0.103)	3.039 (1.432)	8.788 (4.039)
Rocky Side Slope	1.074 (0.556)	5.104 (3.050)	5.559 (3.164)
Savannah	0.327 (0.326)	0.900 (0.761)	1.101 (1.098)
Shallow	0.786 (0.786)	2.041 (1.641)	3.599 (3.457)
Shallow Ridge	0.944 (0.912)	1.721 (0.771)	6.587 (3.210)
Silty	1.660 (1.082)	5.592 (3.529)	2.989 (2.784)
Silty Footslope	0.907 (0.706)	5.072 (2.494)	0.474 (0.449)
Steep Cool Slope	1.613 (1.061)	9.144 (4.029)	4.487 (3.323)
Steep Rocky Side Slope	1.381 (0.728)	8.410 (3.624)	5.759 (1.876)
Steep Warm Slope	0.723 (0.674)	12.961 (2.389)	13.046 (9.986)
Stony Hills	0.115 (0.064)	3.853 (2.075)	1.722 (1.391)
Thin Upland	--	5.304 (1.188)	7.674 (5.916)
Warm Slope	0.113 (0.072)	2.486 (1.581)	9.350 (5.965)
Prairie Dog Colony	--	9.972 (8.233)	1.374 (1.210)

Table 5. Proportion of biomass per range and woodland site that consisted of palatable and unpalatable forbs and grasses in Custer State Park, South Dakota, 2005–2008.

Range or woodland site	Palatable grass	Unpalatable grass	Palatable forbs	Unpalatable forbs	Total palatable	Total unpalatable
Clayey	0.739	0.014	0.209	0.009	0.977	0.023
Cool slope	0.589	0.012	0.340	0.007	0.980	0.020
Overflow	0.692	0.030	0.124	0.016	0.954	0.046
Rocky side slope	0.561	0.137	0.194	0.006	0.858	0.142
Savannah	0.698	0.021	0.186	0.003	0.976	0.024
Shallow	0.686	0.008	0.188	0.002	0.990	0.010
Shallow ridge	0.795	0.032	0.129	0.017	0.951	0.049
Silty	0.561	0.030	0.301	0.011	0.959	0.041
Silty footslope	0.511	0.172	0.169	0.007	0.819	0.181
Steep cool slope	0.575	0.010	0.274	0.078	0.912	0.088
Steep rocky side slope	0.426	0.126	0.286	0.014	0.860	0.140
Steep warm slope	0.365	0.036	0.363	0.012	0.952	0.048
Stony hills	0.648	0.033	0.202	0.005	0.962	0.038
Thin upland	0.613	0.061	0.201	0.000	0.939	0.061
Warm slope	0.804	0.019	0.128	0.008	0.973	0.027
Prairie dog	0.466	0.000	0.505	0.017	0.983	0.017

Table 6. Proportion of biomass for each range site consisting of historic climax community, grazing-induced species, and those species indicative of continued heavy grazing based on data from the Natural Resource Conservation Service, Custer State Park, SD.

Range or woodland site	Historic climax community	Grazing-induced species	Continued overgrazing
Clayey	0.266	0.127	0.000
Overflow	0.040	0.418	0.000
Savannah	0.256	0.079	0.000
Shallow	0.119	0.025	0.141
Silty	0.195	0.279	0.000
Stony hills	0.054	0.420	0.038
Thin upland	0.110	0.029	0.000

Table 7. Proportion of biomass for each range or woodland site consisting of cool-season and warm-season grasses, forbs, and shrubs and comparison to expected species distributions based on NRCS data, Custer State Park, SD, 2005-2008.

	Observed				Expected				
Range or woodland site	Cool-season grass	Warm-season grass	Forb	Shrub	Cool-season grass	Warm-season grass	Forb & shrub	Chi-square statistic	P value
Clayey	0.521	0.191	0.218	0.029	0.70	0.25	0.05	17.5	<0.0001
Cool slope	0.504	0.062	0.347	0.051					
Overflow	0.600	0.043	0.140	0.138	0.35	0.45	0.20	38.9	<0.0001
Rocky side slope	0.426	0.159	0.199	0.103					
Savannah	0.118	0.512	0.190	0.092	0.00	0.75	0.25	15.2	<0.0001
Shallow	0.376	0.243	0.190	0.116	0.15	0.60	0.25	33.8	<0.0001
Shallow ridge	0.297	0.408	0.146	0.028					
Silty	0.305	0.259	0.311	0.097	0.65	0.25	0.10	30.1	<0.0001
Silty footslope	0.436	0.099	0.176	0.139					
Steep cool slope	0.166	0.387	0.352	0.063					
Seep rocky side slope	0.289	0.143	0.300	0.147					
Steep warm slope	0.223	0.172	0.375	0.224					
Stony hills	0.449	0.177	0.207	0.112	0.25	0.55	0.20	25.9	<0.0001
Thin upland	0.416	0.174	0.202	0.124	0.30	0.70	0.00	63.4	<0.0001
Warm slope	0.437	0.230	0.136	0.041					
Prairie dog	0.185	0.236	0.522	0.012					

Table 8. Final model to predict forage production for Custer State Park, SD, based on deviance ratio tests and AIC scores (response variable = ln(kg/ha)).

Variable	Estimate	Standard Error	T-value[c]	P-Value
Intercept	6.477	0.865	7.49	<0.0001
Spring Precipitation Current Year	0.151	0.015	9.93	<0.0001
Spring Precipitation Previous Year	0.082	0.023	3.53	0.0005
Ordinal Frost Date	-0.024	0.003	-7.09	<0.0001
Canopy Cover (PS)[a]	-0.055	0.008	-6.68	<0.0001
Slope	-0.008	0.003	-3.07	0.0022
Elevation	0.002	0.001	2.02	0.0443
Elevation^2	-9.89E-07	<0.001	n/a	<0.0001
Prairie Dog Colony (0,1)[b]	0.438	0.118	3.71	0.0002

[a] PS = psuedo-threshold form of variable; [b] = parameter estimates are for “off” prairie dog colony; [c] degrees of freedom = 461

Table 8, Continued.

Variable	Estimate	Standard Error	T-value[c]	P-Value
Clayey[c]	0.477	0.164	2.92	0.0037
Cool Slope[c]	0.344	0.161	2.14	0.0329
Overflow[c]	1.04	0.158	6.58	<0.0001
Rocky Side Slope[c]	0.22	0.134	1.64	0.1026
Savannah[c]	0.587	0.17	3.44	0.0006
Steep Cool Slope[c]	0.097	0.148	0.66	0.5116
Silty Footslope[c]	0.135	0.188	0.72	0.4735
Shallow[c]	0.409	0.156	2.62	0.009
Shallow Ridge[c]	0.335	0.145	2.31	0.0214
Silty[c]	0.585	0.152	3.86	0.0001
Steep Rocky Side Slope[c]	0.193	0.15	1.29	0.1981
Stony Hills[c]	0.651	0.122	5.33	<0.0001
Steep Warm Slope[c]	-0.198	0.193	-1.03	0.3042
Thin Upland[c]	0.646	0.151	4.27	<0.0001
Warm Slope[c,d]	n/a	n/a	n/a	n/a

[c] all categorical levels of the range site variable; [d] = parameter estimate included in intercept term; [c] degrees of freedom = 461

Table 9. Mean bias error (MBE) and root mean-squared error (RMSE) between predicted and observed biomass at sampling sites in Custer State Park, South Dakota, based on the empirical and modified-NRCS models and the unmodified NRCS production estimates, 2005–2008. Standard error in parentheses.

	Empirical Model		Modified NRCS Model		Unmodified NRCS	
Range or woodland site	MBE	RMSE	MBE	RMSE	MBE	RMSE
Clayey	-280.3 (37.6)	882.7 (31.5)	574.1	1239.6	-9.3	1165.8
Cool slope	-36.1 (27.8)	509.5 (27.5)	-251.1	744.1	-373.5	878.2
Overflow	-966.4 (40.1)	1609.1 (43.9)	1489.5	1962.2	-868.2	1602.8
Rocky side slope	-145.2 (14.1)	492.8 (7.3)	145.1	770.4	70.7	782.7
Savannah	-219.3 (32.1)	812.0 (37.8)	386.3	946.9	-168.5	1135.7
Shallow	-28.4 (27.0)	501.9 (15.3)	152.8	766.9	-413.3	1035.1
Shallow ridge	-163.4 (35.7)	720.5 (27.2)	-301.5	884.5	-482.8	957.1
Silty	-422.6 (63.0)	1388.8 (122.0)	716.7	1703.4	-82.8	1695.8
Silty footslope	-511.3 (28.1)	870.0 (21.2)	-150.8	734.8	-281.3	822.9
Steep cool slope	-203.2 (19.5)	536.2 (12.0)	-204.4	617.5	-233.7	697.3
Steep rocky side slope	-383.0 (39.5)	921.8 (49.0)	-314.7	942.6	-90.5	920.9
Steep warm slope	-891.9 (131.3)	2237.5 (226.8)	-1073.8	2778.5	-1160.2	2805.5
Stony hills	-474.4 (31.5)	1911.7 (105.4)	472.0	1706.0	-790.6	1882.3
Thin upland	-377.8 (24.7)	757.1 (19.8)	104.1	725.5	-787.1	1110.7
Warm slope	-118.4 (29.7)	587.9 (43.9)	-453.5	950.1	-466.2	949.3
Overall	-335.9 (10.2)	1305.8 (35.4)	139.9	1282.1	-410.7	1328.4

Table 10. Biomass production estimates per range and woodland sites in Custer State Park, South Dakota, for the empirical and modified NRCS models, 2005–2008, and for an average weather year.

	2005		2006		2007		2008		Average	
Range or woodland site	Empirical	NRCS	Empirical	NRCS	Empirical	NRCS	Empirical	NRCS	Empirical	NRCS
Clayey	643,953	725,834	681,898	889,351	940,621	773,980	1,185,777	837,570	1,052,425	908,428
Cool slope	634,336	434,806	671,714	532,759	926,573	463,647	1,168,067	501,740	1,036,707	544,188
Overflow	1,618,700	1,693,877	1,714,080	2,075,477	2,364,432	1,806,236	2,980,677	1,954,636	2,645,472	2,119,996
Rocky side slope	4,367,026	6,333,075	4,624,349	7,759,805	6,378,906	6,753,171	8,041,450	7,308,007	7,137,115	7,926,258
Savannah	335,767	335,223	355,552	410,742	490,455	357,459	618,282	386,828	548,751	419,553
Shallow	363,443	301,966	384,859	369,993	530,881	321,996	669,245	348,451	593,982	377,929
Shallow ridge	662,106	494,805	701,120	606,275	967,137	527,626	1,219,203	570,976	1,082,092	619,280
Silty	1,254,285	1,857,986	1,328,193	2,276,556	1,832,132	1,981,231	2,309,643	2,144,009	2,049,903	2,325,390
Silty footslope	29,743	41,757	31,496	51,164	43,446	44,527	54,769	48,185	48,610	52,261
Steep cool slope	123,038	98,705	130,288	120,942	179,722	105,252	226,563	113,900	201,084	123,536
Steep rocky side slope	2,381,879	3,420,419	2,522,229	4,190,974	3,479,206	3,647,306	4,385,996	3,946,966	3,892,751	4,280,875
Steep warm slope	336,960	234,228	356,815	286,996	492,196	249,765	620,478	270,286	550,700	293,152
Stony hills	3,990,449	4,128,467	4,225,582	5,058,537	5,828,841	4,402,322	7,348,020	4,764,013	6,521,668	5,167,044
Thin upland	19,074	12,399	20,198	15,192	27,861	13,222	35,123	14,308	31,173	15,518
Warm slope	448,939	299,995	475,392	367,579	655,765	319,895	826,677	346,178	733,710	375,464
Prairie dog colony	216,785	372,410	229,559	456,307	316,657	397,113	399,188	429,740	354,296	466,095
Total (kgs)	17,437,973	20,789,994	18,465,48	25,473,60	25,471,61	22,169,061	32,110,31	23,990,458	28,499,21	26,020,027

Table 11. Maximum likelihood estimates and standard errors for parameters of most-supported model to explain the difference between spatially-explicit estimates of biomass in Custer State Park, South Dakota, for an average climate year using the empirical and modified NRCS models.

Variable	Maximum likelihood estimate	Standard error
Intercept	0.513	0.206
Clayey[a]	0.000	0.000
Cool slope[a]	0.136	0.030
Overflow[a]	0.184	0.026
Rocky side slope[a]	1.214	0.064
Savannah[a]	0.581	0.019
Shallow[a]	0.679	0.021
Shallow ridge[a]	0.997	0.025
Silty[a]	1.325	0.027
Silty footslope[a]	0.437	0.015
Steep cool slope[a]	0.654	0.018
Steep rocky side slope[a]	3.428	0.054
Steep warm slope[a]	1.545	0.026
Stony hills[a]	2.862	0.040
Thin upland[a]	0.221	0.012
Warm slope[a]	1.830	0.028
Prairie dog colony[a]	0.088	0.022
Slope	-0.118	0.016

[a] all categorical levels of the range site variable

Table 12. 95% Confidence intervals for shrub biomass per range and woodland site in Custer State Park, South Dakota, 2005–2008.

Range or woodland site	Beaked hazel	Bearberry	Birch spp.	Chokecherry	Gooseberry	Green ash	Leadplant
Clayey	0.0000–0.0177	--	--	0.0000–0.0369	--	0.0000–0.0172	0.0245–0.1261
Silty footslope	0.0000–0.0071	0.0000–0.0606	0.0000–0.0349	--	--	--	--
Silty	--	--	--	--	--	--	0.0115–0.0729
Shallow ridge	--	--	--	0.0000–0.0026	--	--	0.0011–0.0079
Shallow	--	--	--	--	--	--	0.0000–0.2445
Steep cool slope	--	--	--	0.0000–0.1299	--	--	0.0000–0.0537
Savannah	--	--	--	0.0000–0.0017	--	--	0.0000–0.1370
Rocky side slope	0.0000–0.0004	0.0000–0.1635	--	--	--	0.0000–0.0524	0.0000–0.0002
Overflow	--	0.0000–0.0846	0.0000–0.0500	--	--	0.0000–0.0007	--
Cool slope	--	--	0.0000–0.0011	0.0000–0.3795	--	--	0.0000–0.1279
Steep rocky side slope	0.0000–0.0150	0.0000–0.1214	0.0000–0.0365	--	0.0000–0.0011	--	0.0000–0.0094
Warm slope	--	--	--	--	--	--	0.0000–0.0871
Thin upland	--	--	--	--	0.0000–0.0036	--	0.0001–0.0015
Steep warm slope	0.0000–0.0383	--	--	0.0000–0.0179	--	0.0000–0.0357	0.1370–0.3270
Stony hills	--	--	--	0.0000–0.0051	--	--	0.0000–0.3852

Table 12, Continued.

Range or woodland site	Mt. mahogany	Oak spp.	Ponderosa pine	Raspberry	Red currant	Rose spp.	Serviceberry
Clayey	--	0.0000–0.0223	0.0711–0.1224	--	--	0.0000–0.1233	--
Silty footslope	--	0.0000–0.0008	0.0205–0.8261	0.0000–0.0490	--	0.0000–0.0187	--
Silty	--	--	0.0000–0.2131	--	--	0.0234–0.0731	--
Shallow ridge	--	0.0000–0.1683	0.0000–0.0749	0.0000–0.1402	--	0.0000–0.0972	--
Shallow	--	--	0.0000–0.5342	0.0000–0.0482	--	0.0033–0.1554	--
Steep cool slope	--	0.0000–0.1930	0.0011–0.0781	--	--	--	0.0000–0.0012
Savannah	--	--	0.0000–1.3670	0.0000–0.0097	--	0.0000–0.0183	--
Rocky side slope	--	--	0.0000–0.6919	0.0000–0.0719	--	0.0000–0.0003	--
Overflow	--	--	0.0000–0.2411	0.0000–0.1598	--	0.0000–0.0241	--
Cool slope	--	0.0000–0.2533	0.0000–0.0904	--	0.0000–0.0072	--	0.0000–0.0188
Steep rocky side slope	--	--	0.0481–0.9870	0.0476–0.1730	0.0000–0.0002	0.0000–0.0042	--
Warm slope	--	0.0000–0.0003	0.0000–0.5216	--	--	0.0000–0.0012	--
Thin upland	--	0.0000–0.0303	0.0000–1.0421	--	--	0.0000–0.0305	--
Steep warm slope	0.000–0.0274	0.0000–0.4376	0.0000–1.7597	0.0000–0.3011	0.0000–0.0056	0.0000–0.0034	--
Stony hills	--	0.0000–0.0004	0.0000–0.1734	0.0000–0.0023	--	0.0000–0.0423	0.0000–0.0026

Table 12, Continued.

Range or woodland site	Skunkbrush	Snowberry	Wild spirea	Winterfat
Clayey	0.0000–0.0349	0.0000–0.0904	--	--
Silty footslope	--	0.0000–0.1321	0.0000–0.0034	--
Silty	--	0.0000–0.1142	--	0.0000–0.0025
Shallow ridge	0.0008–0.0348	0.0000–0.0221	--	0.0000–0.0009
Shallow	0.0000–0.0723	0.0000–0.0362	--	--
Steep cool slope	0.0000–0.0423	0.0000–0.0101	--	--
Savannah	--	--	--	--
Rocky side slope	--	0.0011–0.0270	0.0000–0.0003	--
Overflow	--	0.0113–0.3010	0.0000–0.0010	--
Cool slope	0.0000–0.0042	0.0000–0.3596	--	--
Steep rocky side slope	--	0.0012–0.0661	0.0000–0.0045	--
Warm slope	0.0000–0.0001	0.0000–0.1025	0.0002–0.0007	--
Thin upland	--	0.0046–0.2432	--	--
Steep warm slope	0.0000–0.0207	0.0000–0.0003	--	--
Stony hills	0.0000–0.0038	0.0000–0.1065	--	0.0000–0.0004

Table 13. Shrub biomass (kg) production for Custer State Park, SD, estimated with an empirical forage production model based on herbaceous sampling plots using average climatic conditions, 2005–2008.

Range or woodland site	Aspen	Bearberry	Chokecherry	Gooseberry	Juniper	Leadplant
Clayey	--	--	--	--	--	594
Cool slope	--	--	--	--	--	--
Overflow	--	127848	--	--	--	--
Rocky side slope	15841	334274	--	54244	--	--
Savannah	--	--	--	--	--	5661
Shallow	--	--	--	--	--	32881
Shallow ridge	--	--	27376	11	--	--
Silty	--	1383	--	--	--	24571
Silty footslope	--	--	1174	--	--	--
Steep cool slope	--	--	4471	--	--	2420
Steep rocky side slope	--	145313	--	--	--	59575
Steep warm slope	--	--	--	--	126923	--
Stony hills	--	--	--	--	--	543890
Thin upland	--	--	--	--	--	--
Warm slope	--	--	--	--	--	1266
Prairie dog colony	--	--	--	--	--	--
TOTAL (kg)	15841	608818	33021	54255	126923	670859

Table 13, Continued.

Range or woodland site	Ponderosa pine	Red currant	Rose spp.	Raspberry	Snowberry	Winterfat
Clayey	--	--	--	--	14291	--
Cool slope	--	--	--	--	22318	--
Overflow	61250	--	9325	5138	284754	--
Rocky side slope	314424	48	--	142379	69125	--
Savannah	104013	--	--	17807	--	--
Shallow	30138	--	12384	--	2473	--
Shallow ridge	--	--	--	2003	--	--
Silty	32897	--	107076	--	37436	--
Silty footslope	9673	--	126	262	808	--
Steep cool slope	--	289	--	--	9863	158
Steep rocky side slope	415234	36478	16445	177037	53102	--
Steep warm slope	151410	--	--	52512	26672	--
Stony hills	16	--	105572	16811	171996	--
Thin upland	3235	--	37	--	1991	--
Warm slope	15596	--	--	1666	21085	--
Prairie dog colony	--	--	3272	--	858	445
TOTAL (kg)	1137886	36815	254236	415615	716771	603

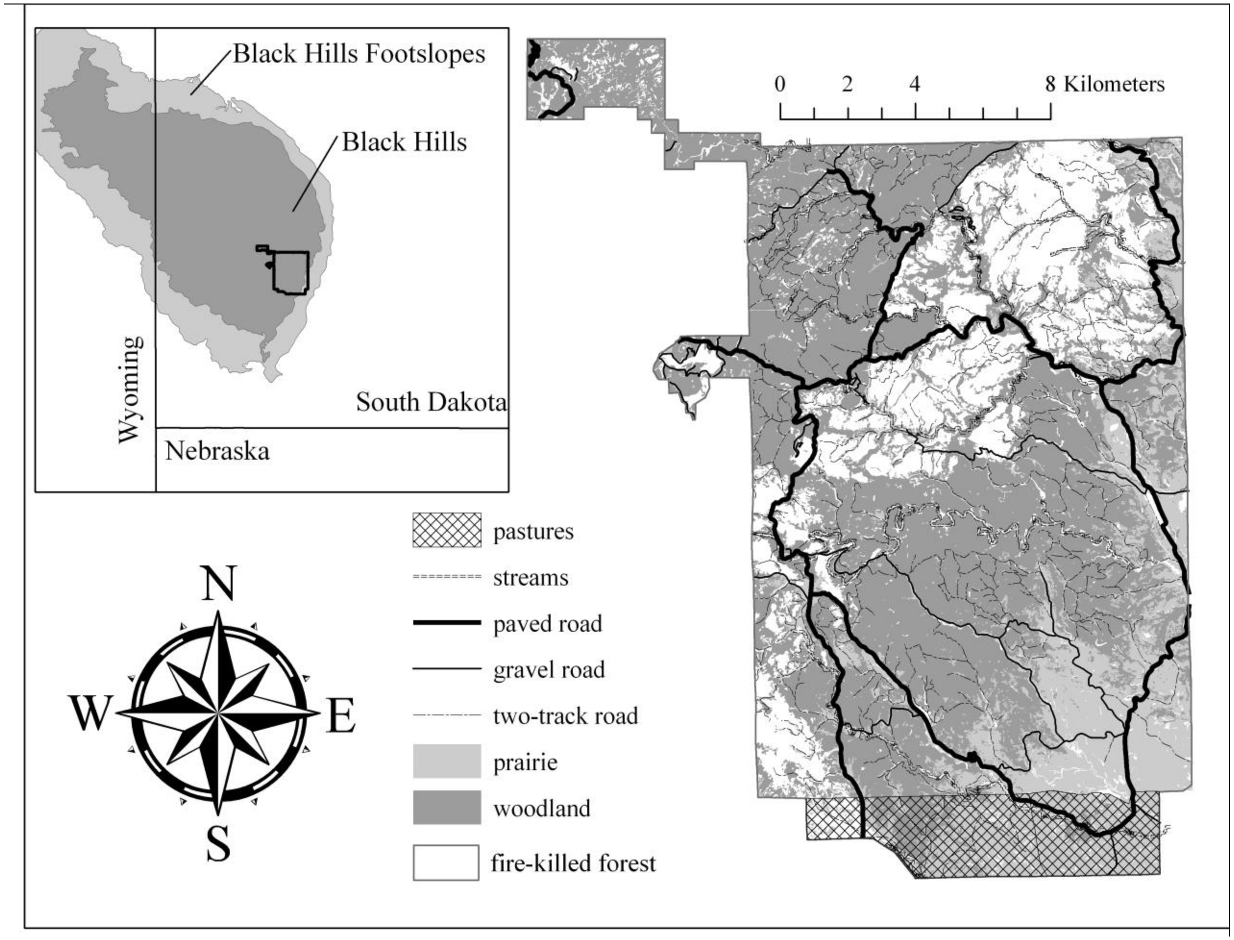

Figure 1. Major features and habitat types of Custer State Park, SD.

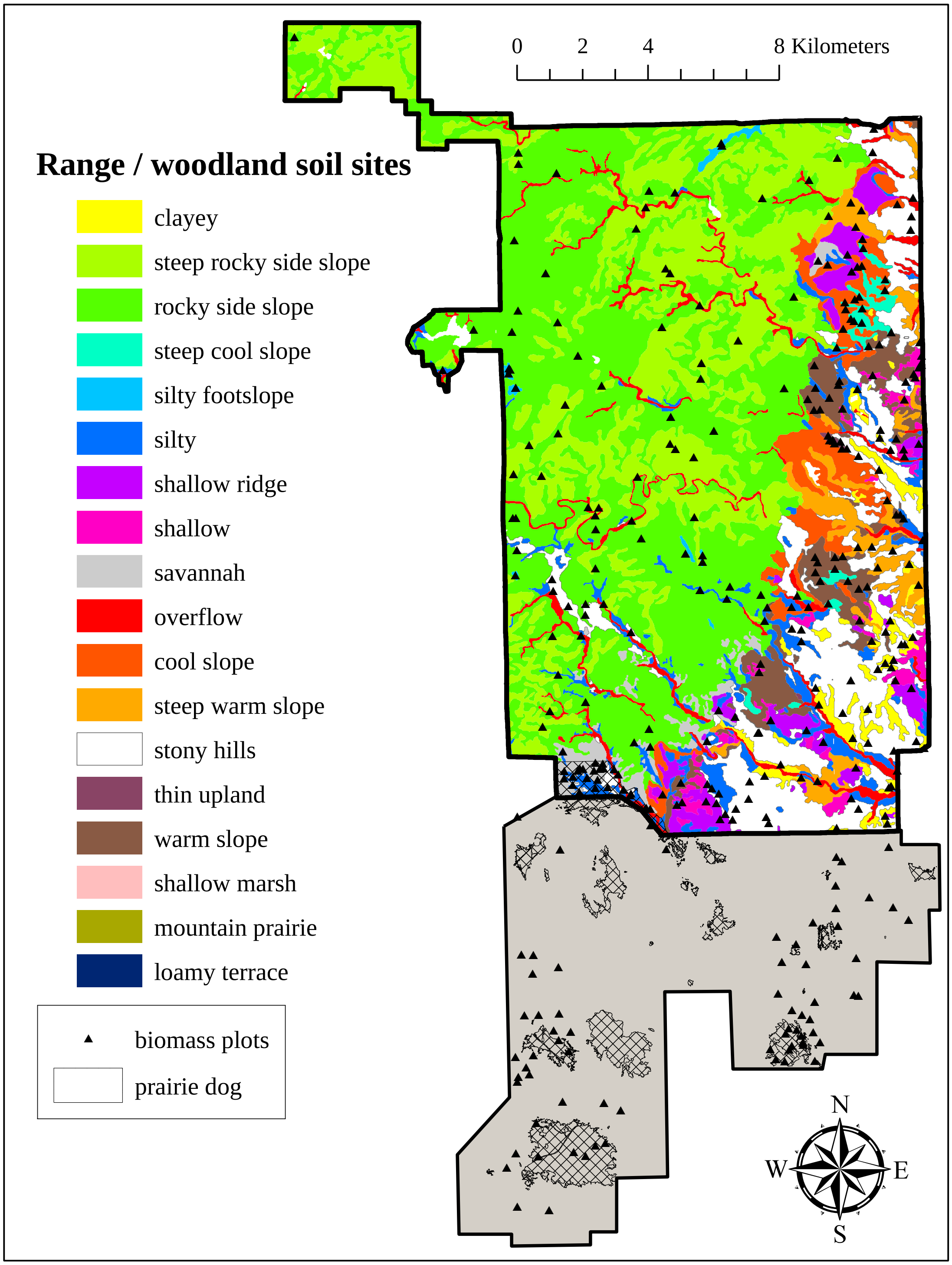

Figure 2. Range and woodland grazable sites and location of biomass sampling sites in Custer State Park and Wind Cave National Park, SD, 2005-2008.

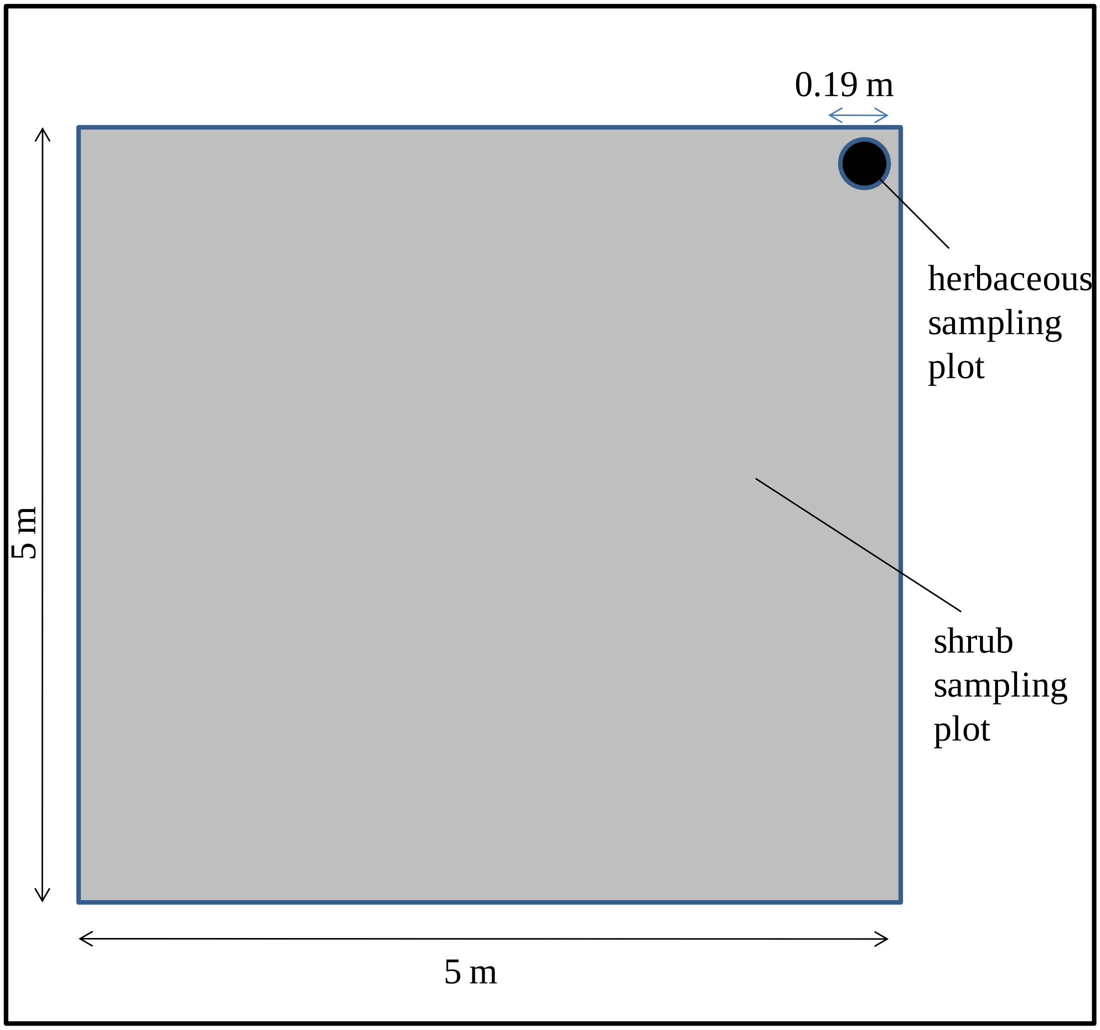

Figure 3. Location of shrub sampling plot in relation to herbaceous sampling plot in Custer State Park, SD.

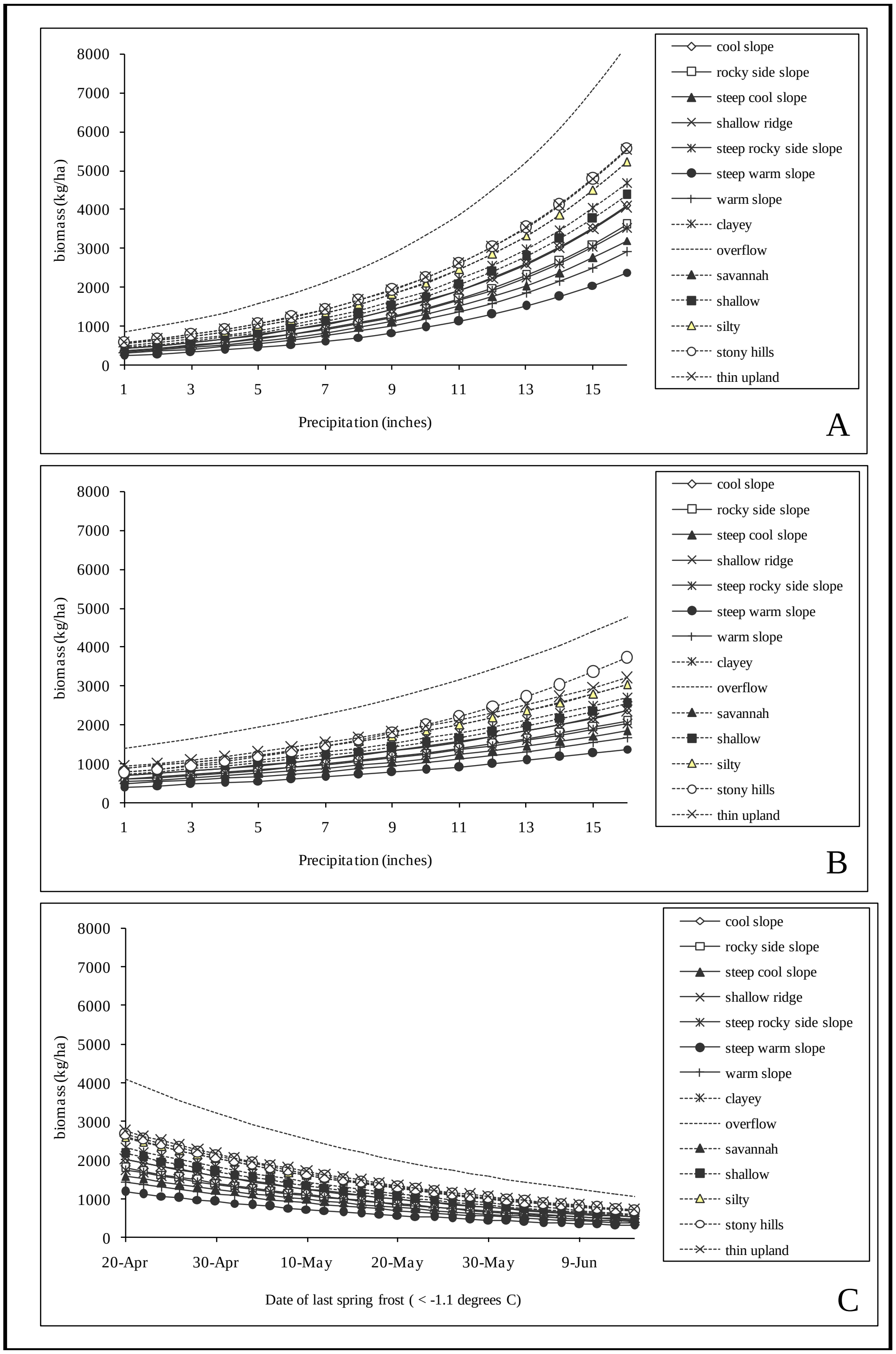

Figure 4. Response of forage production per range and woodland site to changes in current year spring precipitation (A), previous year spring precipitation (B), and date of last spring frost (C; assuming no canopy cover, mean slope, and mean elevation), based on best model to predict forage production 2005–2008 in Custer State Park, SD.

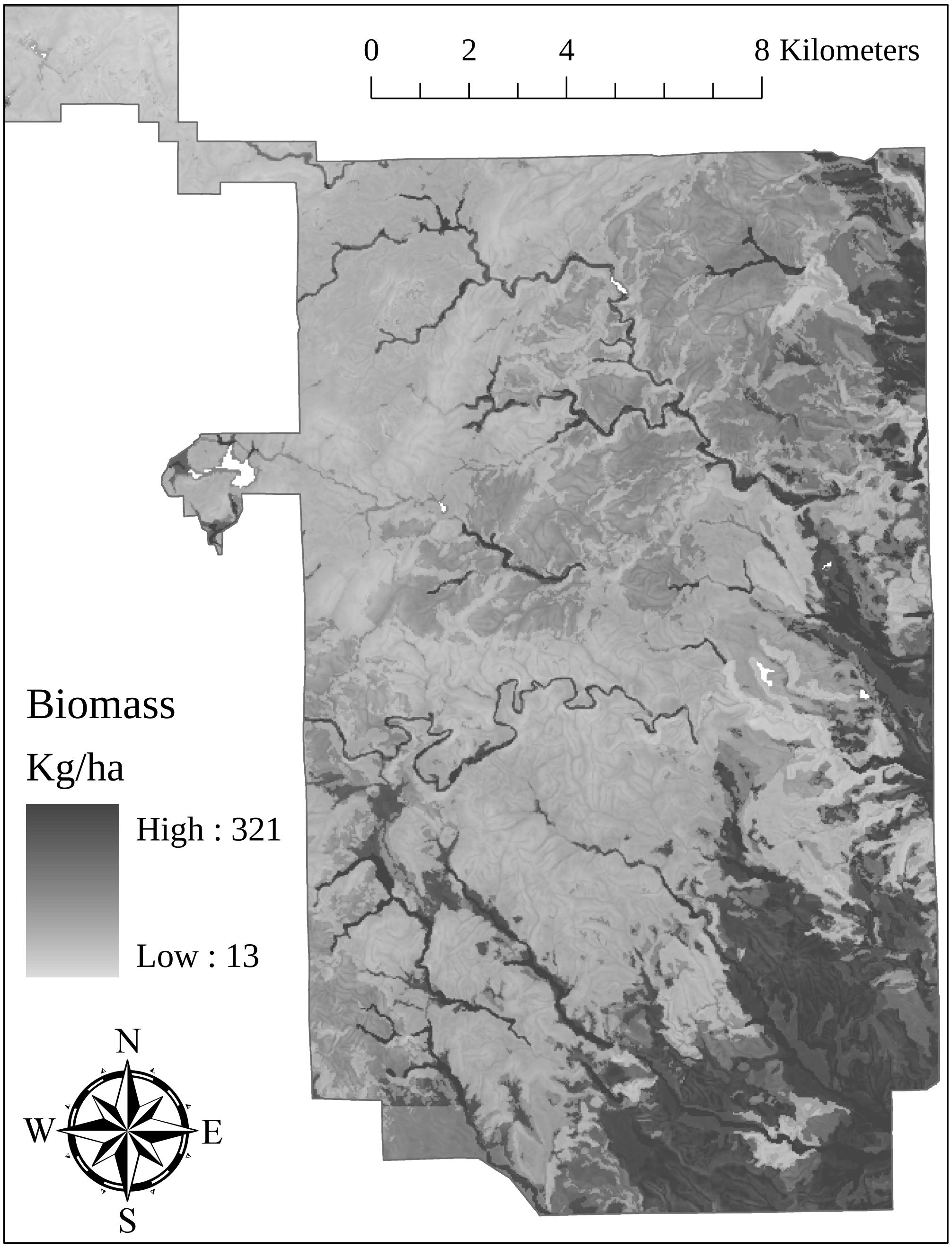

Figure 5. Spatially-explicit forage production based on best predictive model, 25-year mean (1984-2008) for spring precipitation and the mean date of last spring frost from 2004-2008 for Custer State Park, SD.

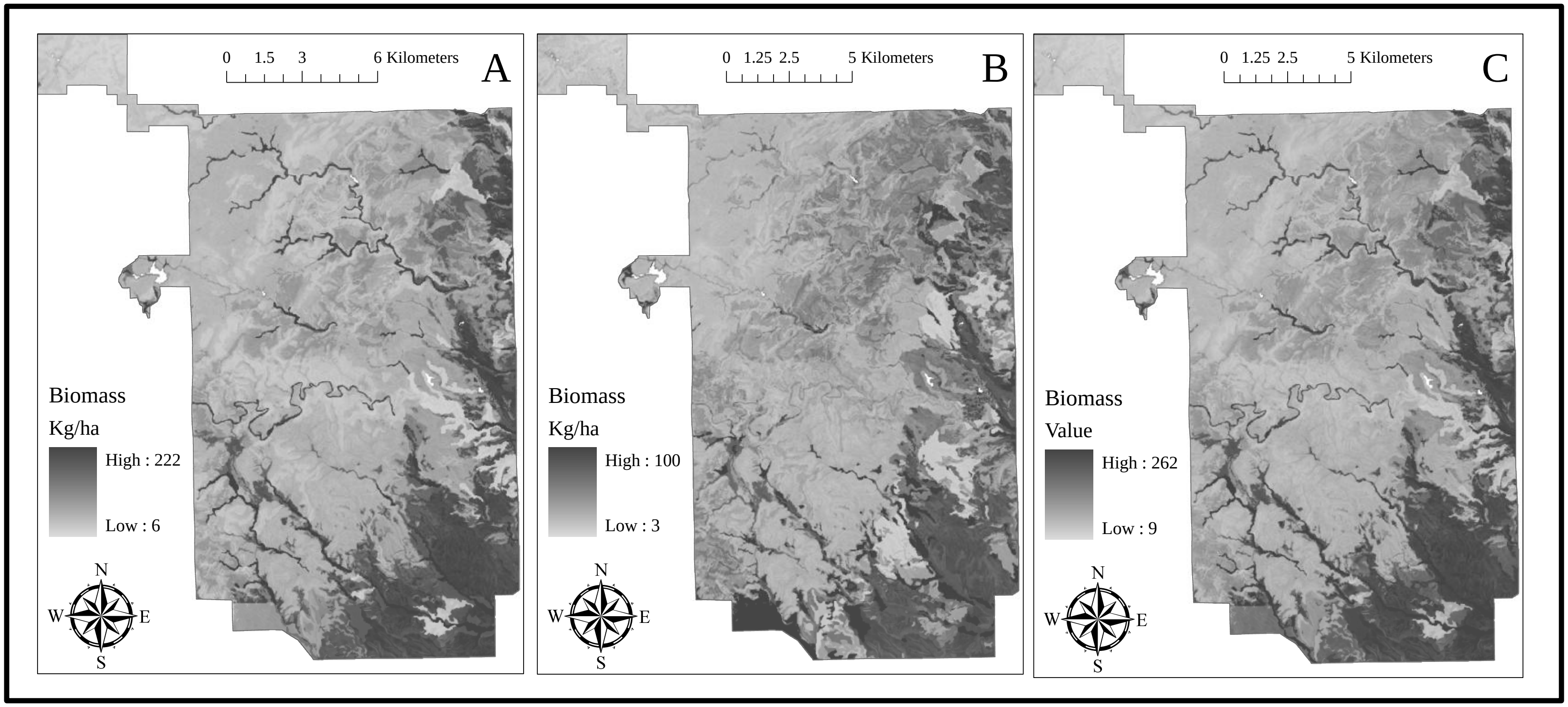

Figure 6. Spatially-explicit palatable grass (A), forb (B), and total forage (C) production based on best predictive model (Table 2), 25-year mean (1984-2008) for spring precipitation, the mean date of last spring frost 2004-2008, and porportion of palatable production per range and woodland site for Custer State Park, SD.

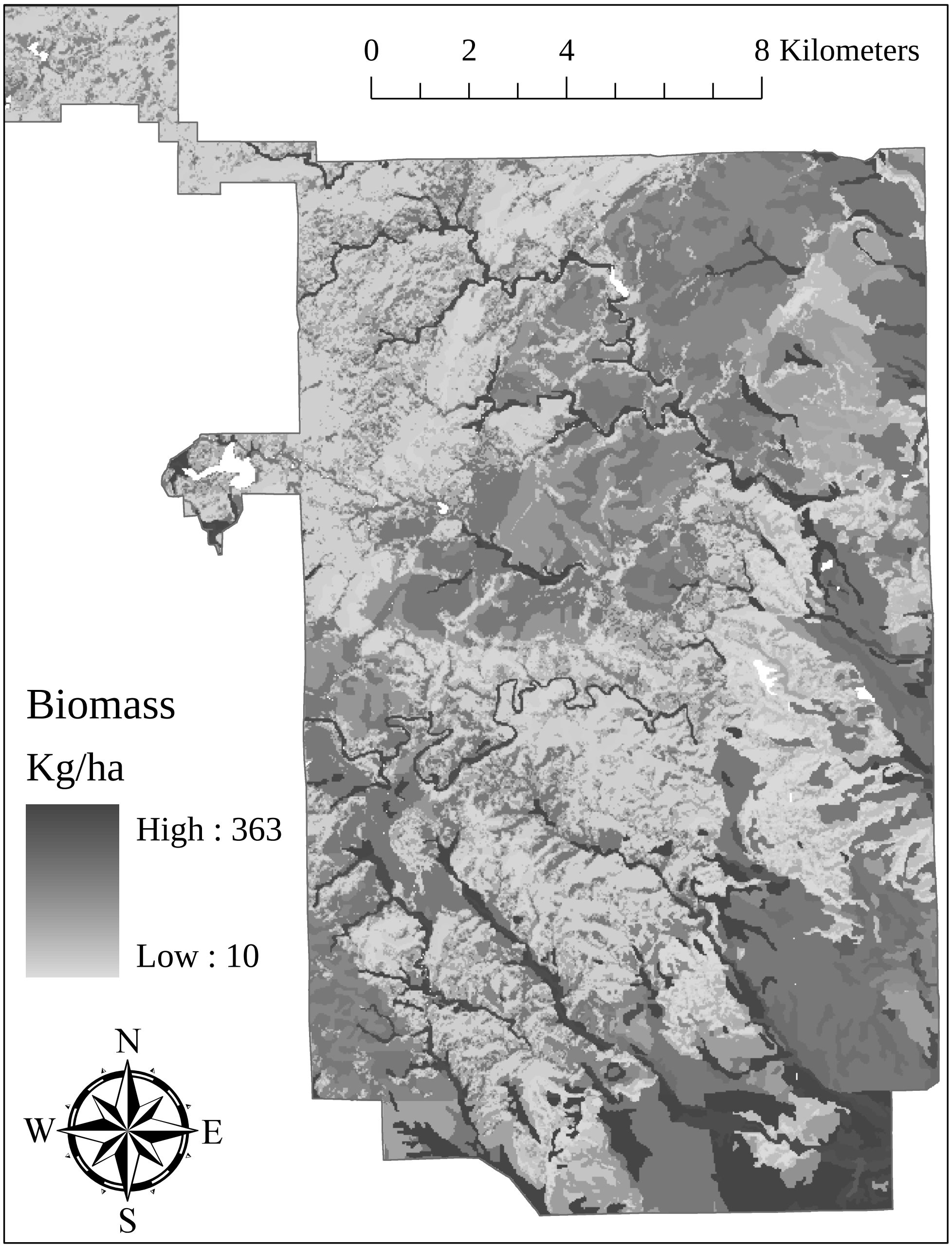

Figure 7. Spatially-explicit forage production based on modified NRCS estimates of forage production per range and woodland grazable site, assumptions of production on steep soil units, and assuming 2 consectutive years of normal precipitation for Custer State Park, SD.

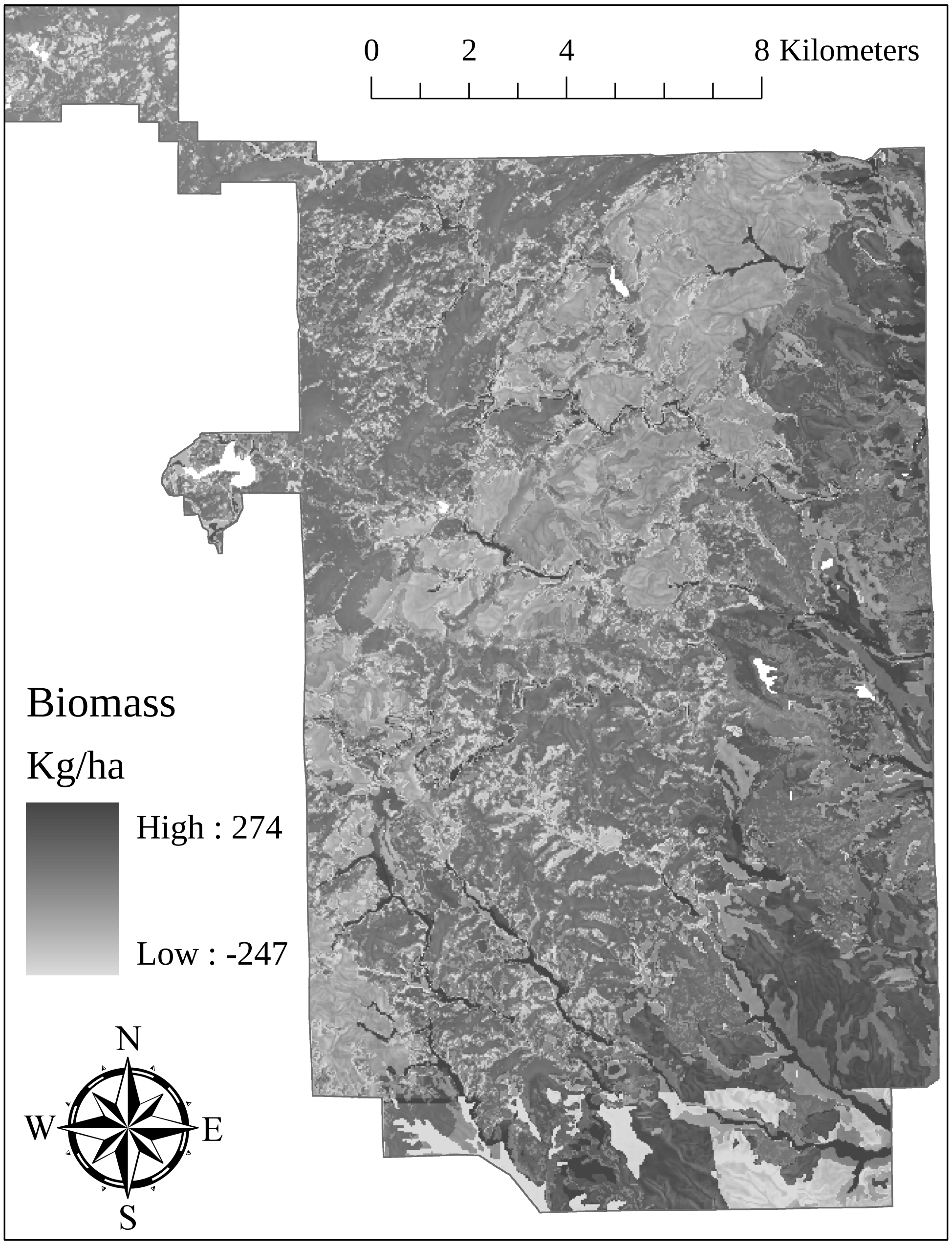

Figure 8. Spatially-explicit differences between empirical and the modified NRCS forage production models (empirical model - NRCS model), based on normal climate conditions for Custer State Park, SD.

CHAPTER II. FACTORS AFFECTING BISON RESOURCE SELECTION IN THE BLACK HILLS, SOUTH DAKOTA.

ABSTRACT

Management of closed bison (*Bison bison*) populations is often confounded by a lack of large scale migration and an absence of predation. Without active management, resource degradation can occur from overgrazing. Although information on resource selection is important to evaluate carrying capacity for bison populations, relatively little research has assessed the mechanisms influencing bison resource selection, or evaluated individual variation in bison resource selection. We radio-tagged 24 adult bison females and 10 adult bison males and collected 9,537 locations from October 2005 – August 2008 in Custer State Park, South Dakota. We developed utilization distributions for each individual by season and year, and ranked 12 *a priori* models related to prevailing hypotheses about bison habitat-relationships, based on their ability to account for differential space use within each bison's home range. We combined individual models and developed seasonal population-level resource selection models that we used to predict bison occurrence throughout the Park. We observed considerable individual heterogeneity in the mechanisms affecting male and female bison resource selection. During every season, female bison occurred in areas that support high forage biomass, including the mixed-grass prairie and upland shrubland habitat types in CSP. However, differences in seasonal selection did occur. Female bison selected areas close to mineral

sites during winter and spring, areas away from unpredictable disturbances during the spring, and areas close to ponds during the summer. Male bison also selected areas of high forage biomass during the non-breeding season, but occurred further from mineral sites and ponds, and close to streams. Although the high amount of heterogeneity and low sample size of male bison resource selection resulted in low predictive ability of population-level probability of occurrence maps, the probability of occurrence maps for female bison performed well based on *k*-fold cross-validation. These results indicate bison herds are likely to change foraging patterns in relation to unique seasonal stressors and changes in palatable forage availability. Artificial mineral sites and water sources can be used to manipulate bison grazing patterns, and we advise monitoring of these areas to prevent habitat degradation in CSP. Limiting the amount of unpredictable disturbance, or allowing disturbance-free areas, during the calving season may be beneficial to female bison with young. Further, the amount of heterogeneity we found in bison resource selection suggests analyses that pool locations across individuals will likely miss the full suite of factors affecting resource selection of ungulates, including gregarious species that form large groups.

INTRODUCTION

Conservation of bison (*Bison bison*) populations presents unique challenges for wildlife managers. The near-extinction and subsequent recovery of the bison in the early 1900s, a result of efforts by William Hornaday, the United States National Zoo, and other private ranchers (Andrei 2005), is one of the earliest and most well-publicized stories of conservation success in North America. Bison are now highly-valued components of the fauna in several State and National Parks in the United States and Canada (Loomis 2004).

However, although bison are no longer considered endangered, their current range has been reduced from vast expanses of the Great Plains to several dozen disjunct public and numerous private herds (Berger and Cunningham 1994). Natural processes such as large scale migration and predation by large carnivores no longer exist in most populations today, and maintaining a balance between range condition and bison population goals is a key objective in many parks containing the species. Identifying and monitoring selected resources is important to prevent over-utilization of those resources, prescribe appropriate stocking rates, and identify resources important to bison conservation.

Despite the importance of resource selection to bison management, there are few studies that address mechanisms affecting space use patterns. Of 182 publications concerning bison retrieved from a literature search (EBSCO Host Academic Search), only 18 (9.8%) of publications addressed bison habitat use or resource selection (B. J. Keller, University of Missouri, unpublished data). Only 2 of these studies (Fortin and Fortin 2009 and Fortin et al. 2009) addressed mechanisms influencing bison resource selection, and none evaluated more than a couple prevailing hypotheses to explain bison resource selection. Descriptive models tend to dominate ungulate resource selection studies, despite the importance of ranking multiple working hypotheses (Romesburg 1981). As a result, we gain information regarding when and where bison occur in specific study areas, but learn little about the overall mechanisms driving bison resource selection as a whole. Further, little information is available regarding individual variation in bison resource selection because most bison habitat use studies use census or survey methodology that pools data across animals. We found only 4 published studies that used information from radio-collared bison (Larter and Gates 1994, Daleszczyk et al. 2007, Fortin et al. 2009, Allred et al. 2011), only two of which (Fortin et al. 2009, Allred et al. 2011) evaluated individual resource selection.

The literature suggests that the quantity and quality of forage are the most important factors affecting bison resource selection (Van Vuren 2001, Stueter et al. 1995). Bison have adapted a foraging strategy based on the consumption of large amounts of relatively poor quality forage. To facilitate this foraging strategy, bison typically occupy broad, open grassland habitat (Wydeven and Dahlgren 1985, Krueger 1986, Steuter et al. 1995) that can support large herds of bison females and juveniles. Within these grassland communities, bison select areas with young, succulent grasses including recently burned areas, grazed areas, and prairie dog (*Cynomys* spp.) colonies (Plumb and Dodd 1993, Steuter et al. 1995, Wallace et al. 1995, Biodini et al. 1999, Schuler et al. 2006). When these areas are not present or when forage quality is low, bison are more likely to forage randomly across the landscape (Wydeven and Dahlgren 1985). Thus, bison grazing patterns may be temporally and spatially dynamic in response to shifts in forage quality across the landscape. Thus, it is critical to quantify this dynamic process to better manage the resource base. Other factors that may influence bison resource selection include predator avoidance (Fortin and Fortin 2009, Fortin et al. 2009) and human disturbance and development (Bjornlie and Garrott 2001, Fortin and Andruskiw 2003, Fortin et al. 2009).

Resource selection could play a particularly important role in bison carrying capacity estimates in large heterogeneous landscapes, such as Custer State Park (CSP), South Dakota, that supports an adult bison population of approximately 800-1000 animals. In addition to bison, the Park maintains pronghorn (*Antilocapra americana*), elk

(*Cervus elaphus*), white-tailed deer (*Odocoileus virginiana*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis canadensis*) populations; thus the potential for range overutilization is high. Park managers manipulate the bison population through controlled culling operations in the fall. Managers determine culling rates based on a forage allocation model that requires information about bison resource use. Refined data about resource selection would help evaluate carrying capacity and associated stocking rates for the bison population in CSP.

Our goal was to predict seasonal bison use CSP and evaluate mechanisms influencing spatio-temporal dynamics of bison resource selection. We tested multiple *a priori* hypotheses to explain individual male and female bison resource selection, and built a seasonal population-level resource selection model for both male and female bison. We determined bison resource selection by season and sex at the home range scale.

STUDY AREA

Custer State Park was a 286.32 km^2 reserve located in southwest South Dakota, approximately 27 km southwest of Rapid City. Custer State Park is composed of a mixture of rangeland and forest common to the southern Black Hills region. Steep granite spires characterize the northwest portion of the Park, undulating forested hills dominate the central portion, and grasslands dominate the eastern and southern portions of the Park (CSP 1995; Figure 1). Elevations range from 1,146–2,042 meters (CSP 1995).

Approximately 55% of CSP is covered by coniferous forest, composed of 2.15 km^2 of ponderosa pine (*Pinus ponderosa*) - white spruce (*Picea glauca*) mixed forest on northern slopes and high elevations and 155.79 km^2 of ponderosa pine forest located throughout the Park (Figure 1). A small amount of deciduous forest (2% of CSP) is characterized by predominantly bur oak (*Quercus macrocarpa*) and paper birch (*Betula papyrifera*) forest that occur primarily in riparian corridors (Figure 1). Stand structure diversity in CSP consists of 52.33 km^2 of single-story forest and 71.49 km^2 of multi-story forest (CSP 1995). Woodland understory communities in CSP are dominated by Kentucky bluegrass (*Poa pratensis*), poverty oatgrass (*Danthonia spicata*), sedges (*Carex* spp.), bearberry (*Arctostaphylos uva-ursi*), wild raspberry (*Rubus ideaus*), and western snowberry (*Symphoicarpus occidentalis*; unpublished data). Almost 30% of CSP is burned-over forest, the results of the Galena fire of 1988, the Cicero Peak fire of 1990, and the four-mile fire of 2008. Fire-damaged forest consists of 109.79 km^2, 60% of which is fire-killed where the canopy remains primarily open (CSP 1995; Figure 1).

Approximately 21% (61.05 km^2) of CSP is northern mixed-grass prairie and upland shrubland (CSP 1995; Figure 1). Grasslands are dominated by the cool-season grasses Kentucky bluegrass and western wheatgrass (*Agropyron smithi*); and the warm-season grasses: big bluestem (*Andropogen gerardi*), little bluestem (*Andropogen scoparius*), blue grama (*Bouteloua gracilis*), and sideoats grama (*Bouteloua curtipendula*; CSP 1995). Important shrub species include leadplant (*Amorpha canscens*), western snowberry, wild raspberry, and wild rose (*Rosa* spp.)

Approximately 4.05 km^2 of CSP are classified as riparian habitat, consisting of 13 watersheds either completely or partially within the Park (CSP 1995). There are 6 streams with constant annual flow, although these streams rarely reach the prairie, and numerous ephemeral and permanent water impoundments in CSP during our study period

(Figure 1). Water impoundments are created in the prairie region specifically for use by bison and other wildlife, or were already present when CSP was created from old ranching operations. Four large reservoirs are present in CSP, although two of these were outside of the fenced portion of the park and unavailable to bison. The other two reservoirs were located outside of the prairie region. There were two solar-driven water troughs located in the prairie region during the study period that provided a constant supply of fresh water for wildlife, and 69 other small permanent and ephemeral ponds. The maximum and average distance to a water source in CSP was 2.73 and 0.69 km, respectively, however many of the emphemeral ponds only contain water during the spring.

Park personnel maintained 10 artificial mineral sites in CSP. These mineral sites were established in the mixed-grass prairie region of CSP and intended for use by bison. Mineral sites were replenished with granular free-choice mineral several times throughout a year and consisted of a mixture of calcium, phosphorus, salt, magnesium, copper, manganese, zinc, vitamin A, vitamin D, and Vitamin E (Hubbard Feeds Inc., Mankato, Minnesota).

For 1992–2008, annual precipitation for CSP averaged 49.86 cm and ranged from 74% to 161% of the 25-year mean. Approximately 76% of precipitation in CSP fell from April to September (Custer State Park, unpublished data). Winter in the southern Black Hills is considerably milder than elsewhere in the region, and a persistent snowpack was not typically present during the study period. Average snowfall for the southern Black Hills is 32.0 cm; March is the snowiest month with an average snowfall of 18.8 cm. Temperatures in CSP are more moderate than the surrounding plains; the average annual,

summer and winter temperature in CSP is 6.7° C, 16° C, and –5° C, respectively (CSP 1995).

Approximately 800–1000 adult bison, 408–718 elk, 163–279 pronghorn, 867 white-tailed deer, 285 mule deer, 38–48 bighorn sheep, and 35–40 feral burros (*Equus asinus*) occupied CSP during our study period (C. Lehman, Custer State Park, personal communication). Bison are culled annually in CSP. Bison females, calves, and young males (generally < 3 years) are herded together and passed through a modified chute system during the fall bison round-up. Animals are culled based on reproductive status, age, and quotas for removal. Adult males (> 3 years) are culled during the fall trophy male hunts. A 1.54 m woven-wire fence surrounded the majority of the CSP except for a small portion of the Park in the Needles and Sylvan Lake area. This fence prevented movement of bison but allowed for movement of all other ungulate species into or out of CSP. There are two other internally fenced areas in CSP, which create three distinct pastures in CSP and are used to move bison during the roundup and to manage grazing of bison throughout the year (Figure 1). Two of these pastures, comprising 13.19 km^2 (4.6% of CSP) and 8.82 km^2 (3.1% of CSP), are off-limits to bison during the summer and fall. Coyotes (*Canis latrans*), mountain lions (*Felis concolor*) and bobcats (*Felis rufus*) are the remaining predators in CSP; both wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) populations have been extirpated from the area.

There is a considerable amount of human-related infrastructure in CSP, consisting of paved, gravel, and two track roads and numerous buildings and campgrounds. There are 90.1 km of paved roads, including one state highway, one US highway, and the Wildlife Loop Road, and 76.5 km of gravel roads open to the public, in CSP. Two-track roads, that are only used by park employees, cover 560.9 km. There are approximately 84 small structures and buildings in the park, six campgrounds, and one small airport. From 2005–2008, an average of 1,631,432 people visited CSP annually. The majority of this visitation (59%) occurred during the summer, followed by fall (20%), spring (16%) and winter (5%; C. Pugsley, Custer State Park, personal communication).

METHODS

Capture and monitoring

We used radio-telemetry to evaluate resource selection of bison. We monitored 35 bison (25 females and 10 males) from October 2005 - August 2008. We radio-collared 24 female bison during the annual fall bison roundup in October 2005. All female and juvenile male bison (generally less than 4 years in age) were collected during the roundup and separated using a modified cattle chute system. We placed radio-collars equipped with mortality sensors (Advanced Telemetry Systems, Isanti, MN, USA) around the necks of adult females as we caught them in the squeeze chute. We caught females at infrequent intervals during the round-up in an attempt to sample a stratified (females > 3 years old) random portion of the population. We purposefully collared 9 bison females already being monitored by CSP for a social status study, which resulted in one dam/offspring pair both receiving radiocollars, but we do not believe this violated the independence of locations as the dam's offspring underwent forced-weaning the fall after its birth. Forcibly-weaned bison calves do not typically re-associate with dams (Brookshier 2000). We determined the age of females by brand number. We released all females into a fenced pasture for approximately 48 hours after capture to ensure calves that were separated during the roundup were re-united with their mothers. After 48 hours, we released the herd into CSP. We collared 1 female during the October 2007 roundup to replace a mortality that occurred.

We captured 10 mature males and tagged each with mortality sensing ear-tag radio-transmitters (Advanced Telemetry Systems, Isanti, MN, USA) during fall 2006 (n = 1) and fall 2007 (n = 9). We selected males between the ages of 4 and 15 years for capture. Because CSP annually harvests most of the available 10-year old males during a trophy hunt, we attempted to capture primarily males < 8 years of age to ensure members of our sample would not be harvested but we did capture one 15-year-old male. We determined ages of males by brand. We located male groups while driving throughout CSP on paved, gravel and two-track roads (Figure 1). Mature male groups do not typically associate with the large female/calf groups (Berger and Cunningham 1994, Mooring et al. 2005), and we captured most of the males in meadows in forested areas along two-track roads.   We attempted to tag males in different groups in different geographical areas of CSP. Males were sedated with a 7 cc mixture of 500 mg of Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, IA, USA) reconstituted with 6 cc of 100 mg/ml xylazine hydrochloride and 1 cc butorphanol. We antagonized this drug mixture with 1 cc of Antisedan® (Pfizer Animal Health, Exton, PA, USA), delivered intravenously. We monitored sedated males until they were resting sternally or standing upright.

Ear-tag transmitters had a life of approximately 9 months and were equipped with mortality sensors. We selected the fall season to place transmitters on bison males so that we could observe resource use outside of the breeding season (when males are with female groups) because information on female herd use was obtained from the radio-collared females, and to prevent damage to ear-tag transmitters due to fights among males during the breeding season, which occurs in late summer.

We located bison approximately 5 times per week, based on a rotating schedule that coincided with sunrise and sunset, October 2005 – August 2008. We separated locations by 25–30 hour intervals, and visually confirmed locations or used triangulation techniques during night sampling periods or when weather conditions did not permit off-road travel. We visually confirmed 75.3% of female bison and 66.5% of male bison locations. Universal Transverse Mercator (UTM) coordinates of collared animals were recorded with a handheld GPS. We only recorded azimuths for triangulation that were < 20 min apart to account for animal movement, and obtained at least 2 azimuths > 45° apart. Telemetry accuracy was evaluated by Millspaugh et al. (2000) for CSP, and mean distance from estimated to true location was 176.1 m (range = 13.4–746.6 m). We used the computer program Location Of A Signal (LOAS; version 4.0, Ecological Software Solutions 2007) to estimate animal locations from two or more azimuths.

Resource selection hypotheses

We evaluated support for 12 *a priori* models for each individual bison UD (Table 1), representing hypotheses based on the literature regarding bison resource selection. We included non-linear forms of explanatory variables when appropriate.

Forage. Forage quantity and quality is generally considered the most important factor affecting bison resource selection. We hypothesized that bison would select areas of high grass biomass, but that the selection of cool-season and warm-season grasses might differ seasonally. The preference of bison for warm-season grasses is well-documented (Peden et al. 1973, Pfeiffer and Hartnett 1995, Plumb and Dodd 1993).

Specifically, we predicted bison would select areas of high cool-season grass biomass during spring and warm-season biomass during the summer, when each of these forage groups are high in nutrition and palatability. This hypothesis was evaluated for both male and female bison resource selection. We used the forage biomass model developed in Chapter 1 to build GIS covariate layers of biomass of cool-season grasses, warm-season grasses, and forbs throughout CSP. The forage biomass model includes parameters for range/woodland grazable site, slope, elevation, canopy cover, prairie dog colony, current annual spring precipitation, previous year spring precipitation, and ordinal date of last spring frost. We used the 25-year mean (1983-2008) for spring precipitation variables and the mean ordinal date of last spring frost for 2004-2008.

Forage and distance to mineral sites. Natural and artificial mineral sites are areas of high use by wild (Jones and Hanson 1984) and domestic (Bailey et al. 2008) ungulates, but little information is available regarding bison and mineral sites. Because we predicted bison to select areas in close proximity to mineral sites, we included a distance to mineral site variable in the original forage model to determine if mineral sites were important to bison selection (Table 1). This hypothesis was evaluated for both male and female bison resource selection.

Water. Bison do not use areas in close proximity to water more than they are available (Coppedge and Shaw 1998), and use water sources less than cattle (Van Vuren 1984, Van Vuren et al. 2001), but bison use water at least once per day (Peden et al. 1973, Norland 1984). Because bison in CSP are frequently observed using ponds (C. Kremer, Custer State Park, personal communication), we hypothesized that bison would select areas close to water. This hypothesis was evaluated for both male and female bison resource selection. The water model consisted of 2 separate parameters, distance from flowing stream, and distance from pond, calculated using Spatial Analyst in ArcGIS 9.2. Coverage of water features was obtained from Cogan et al. (2004).

Forage and water. We thought it was likely that more than 1 mechanism was influencing bison resource selection, so we combined certain logical mechanisms into one hypothesis. We hypothesized that bison would select areas of high forage biomass in close relation to water. We considered distance to all water in general (combined ponds and streams GIS layers) and calculated its inverse to account for the relative closeness of any pixel to a water site. We multiplied the cool-season and warm-season biomass and layers by the inverse water distance layer to create 'warm-season production adjusted by distance to water' and 'cool-season production adjusted by distance to water' layers. These layers consisted of high values when both forage availability and closeness to water were high, and low values when either forage availability or closeness to water were low. This hypothesis was evaluated for both male and female bison resource selection.

Human-related disturbance. Given that human visitation of Custer State Park rivals that of other larger parks, such as Glacier and Grand Teton National Park, we believe it is likely that public visitation is the major source of disturbance in CSP. The response of ungulates to human-related disturbance can vary based on season, predator avoidance strategy, reproductive status, whether it is a hunted or un-hunted population, and whether the disturbance is predictable or unpredictable (Stankowich 2008). The bison population in CSP does experience limited hunting and disturbance related to the roundup each year, so we were unsure the degree to which they habituate to the large amount of human-related disturbance in CSP. We modeled disturbances using features related to human visitation, such as roads and campgrounds. We hypothesized that the response of bison to disturbance depended on its predictability and separated our disturbance hypothesis into predictable, unpredictable and total disturbance subhypotheses. Because public visitation of the park is highly seasonally dependant, bison may have become less habituated to use of certain road types during different seasons. Paved, gravel and two-track roads all occur in CSP (Figure 1). Paved roads were highly traveled during all seasons as two of the three paved roads are federal or state highways. Thus, we classified these areas, along with areas of human activity (e.g., buildings and campgrounds) as having predictable disturbance for every season. We assumed trails and two-track roads that were used by park personnel only acted as areas of unpredictable disturbance during all seasons. However, we hypothesized that the predictability of disturbance on gravel roads varied with season, where the higher occurrence of tourists during spring and summer resulted in more predictable disturbance as compared to fall and winter where gravel roads acted as areas of unpredictable disturbance. This hypothesis was evaluated for both male and female bison resource selection. We computed relative kernel densities of disturbance features to characterize their presence throughout the park. Because kernel density did not account for topographical or vegetative buffering from roads, we included a “visibility” metric in an alternative submodel to all sub-hypotheses. This visibility metric measured the probability that an animal could be viewed from the road based on topographical features and vegetation structure (G. Roloff, University of Michigan, personal communication).

Forage and disturbance. The forage and disturbance hypothesis accounts for the potential of bison to avoid areas of high forage biomass close to areas of human-related disturbance. We hypothesized that bison would select areas of high biomass that were far from human disturbances. We used the total disturbance density layer (described above) and calculated an inverse total disturbance density. We multiplied the cool-season and warm-season biomass layers by the inverse disturbance density layer to create 'cool-season production adjusted by disturbance' and 'warm-season production adjusted by disturbance' layers. These layers consisted of high values when both forage availability and disturbance density were low, and low values when either forage availability or disturbance density were high. This hypothesis was evaluated for both male and female bison resource selection.

Thermal cover and heat avoidance. Bison decrease activity as temperatures increase during the summer and seek out areas to ameliorate heat-related stress (Belovsky and Slade 1986). We hypothesized that bison would seek areas of higher canopy cover and lower solar radiation during the spring and summer, but that the opposite relationship would exist during the fall and winter. Thus, our thermal cover and heat avoidance hypothesis consisted of canopy cover and solar radiation variables. We obtained canopy cover from the National Land Cover Database (Homer et al. 2004). Solar radiation was calculated from the digital elevation model (DEM) using the Area Solar Radiation tool in ArcGIS 9.2. This tool uses variation in elevation, slope, aspect, shadows cast by topographic features, and variation in day and time of year to calculate insolation (Environmental Systems Research Institute 2006). We computed solar radiation separately for each season to account for differences due to day length. This hypothesis was evaluated for both male and female bison resource selection.

Predator avoidance. Although the predator community in CSP likely posed little threat to a healthy adult bison during our study period, bison calves may have been susceptible to predation by mountain lions or coyotes. Furthermore, evolutionary development in a large predator rich environment (e.g. grizzly bears, wolves) may have affected bison resource selection even though little threat currently existed. We hypothesized that the ability of bison to detect and avoid predators in CSP was related to their ability to see the predators and to run away from them. Areas of rugged terrain are associated with predator presence and hiding cover in CSP, and affect the ability of bison to detect and quickly evade predators. If predator avoidance was important to bison resource selection, we predicted that bison would select areas of low terrain ruggedness and far from forests. This hypothesis was evaluated for both male and female bison resource selection. We included a terrain ruggedness and distance to forest variable in our predator avoidance model. Terrain ruggedness was represented by a surface ratio value, that we calculated with DEM Surface Tools extension for ArcGIS (Jenness 2010). Surface ratio was calculated as the ratio of surface area to planimetric area in a pixel from the digital elevation model. This ratio is an indicator of topographic roughness (Jenness 2010). Distance to forest was calculated using forest polygons derived from the Cogan et al. (2004) vegetation coverage database. Areas of rugged terrain are associated with predator presence and hiding cover in CSP, and affect the ability of bison to detect and quickly evade predators.

Habitat type. We included a habitat type model to account for coarse-grained selection by bison in CSP. Bison selection of open grassland habitat (Krueger 1986, Steuter et al. 1995) and prairie dog towns (Coppock et al. 1983) have been documented elsewhere. We hypothesized that bison would select for upland grassland, upland shrubland, wetlands, and prairie dog towns, but that bison use would be negatively associated with all other habitat types. We used the vegetation classification map developed by Cogan et al. (2004) to divide the study area into 11 distinct habitat types: barren, coniferous forest, deciduous forest, floodplain woodland, urban, prairie-dog colony, post-fire vegetation, riparian shrubland, upland grassland, upland shrubland, and wetland herbaceous vegetation. This habitat type raster was used as a categorical explanatory variable in the model. This hypothesis was evaluated for both male and female bison resource selection.

Herd accommodation. We developed this hypothesis to account for bison selection of areas based on whether they could support large herds. Bison selected habitats based on forage availability and ability to support herd size in Steuter et al. (1995). This hypothesis was evaluated for female bison resource selection only because mature males do not form large groups (Berger and Cunningham 1994, Mooring et al. 2005). We predicted that bison would select large contiguous patches of low terrain ruggedness for their ability to support large herds. Bison avoid areas of steep terrain (Berger and Cunningham 1994), and thus larger areas of flat terrain would be able to support larger numbers of bison. This model included variables for patch size and terrain ruggedness. We extracted the lines from the habitat type layer used above, and defined these polygons as ‘patches’, then we used Hawth’s Tools to add the area of each polygon to its attribute table. We used the surface ratio raster described above to represent terrain ruggedness.

Data analysis

Utilization distributions and resource utilization functions. We calculated utilization distributions (UD; Worton 1989) for each individual bison for each season and year. We used the KernSmooth package (Duong 2009) in R (R Development Core Team 2009) to develop fixed-kernel UDs, and used the plug-in option for bandwidth estimation that allows for separate smoothing in x and y directions (Gitzen et al. 2006). We separated locations for each female bison into year and season combinations (fall = 1 September – 31 November; winter = 1 December – 29 February; spring = 1 March – 30 May; summer = 1 June – 30 August) and into non-breeding season (1 September – 1 June) and year combinations for the male bison. Only bison with ≥ 30 locations for each year-season combination were included in the analysis (Seaman et al. 1999). To combine relative use with habitat attribute data, we imported UDs for each individual into a Geographic Information System (GIS). We defined resource use as a 95% probability distribution for the animal (Marzluff et al. 2004) and excluded any portion of the UD that fell outside of the CSP park boundary or into fenced pastures unavailable to bison, due to smoothing.

We used resource utilization functions (RUF; Marzluff et al. 2004) to evaluate resource selection of individual bison in CSP. A RUF is similar to a resource selection function (Manly et al. 2002) but uses a continuous measure of resource use (the UD height) rather than a binary measure (used or unused) based on animal locations. We used the RUF package in R created by Marzluff et al. (2004; available at www.csde.washington.edu/~handcock/ruf/) to fit the models. We used the ruf.fit function to relate the continuous measure of UD height for each individual to the explanatory variables included in each model. The RUF package fits a regression to each animal's UD with spatial correlation as a function of the distance between the pixels, using a stationary model from the Matern class that is function of the Euclidian distance between two locations (Marzluff et al. 2004). In our case, the distance between pixels corresponded to the bandwidth used to estimate each individual's UD. We calculated standardized coefficients for each model (see below).

Model selection. We combined resource attributes into models that represented hypotheses about the mechanisms driving bison resource selection. We ranked these hypotheses by the relative support they had, based on Akaike's information criterion (AIC), to describe the variation in relative use that occurred within each individual's home range. We used AIC to rank models for each individual animal UD, and used model averaging techniques (Burnham and Anderson 1998) when uncertainty occurred among models (> 1 model accounted for 90% of total Akaike weights). We examined the standardized RUF coefficients from the most supported, or model-averaged most supported, model for each bison to compare use of resources among seasons and sex-class. The standardized RUF coefficients are calculated as:

$$\widehat{\beta_j} = \hat{\beta}_{j}^{*} \frac{S_{xj}}{s_{\mathrm{RUF}}}$$

where $\hat{\beta}_{j}^{*}$ is the maximum likelihood estimate of $\widehat{\beta_j}$, the partial regression coefficient from the multiple regression equation; S_{xj} is the standard deviation of the values of resource *j*; and the s_{RUF} is the estimate of the standard deviation of the UD heights (Marzluff et al. 2004). Standardized coefficients allow comparisons of the relative influence of resources on bison habitat use (Marzluff et al. 2004). For each individual, we averaged standardized RUF coefficients for the most supported model among years for each season. We estimated a population-level RUF model for each season by averaging the standardized RUF coefficients for the across-year model for each individual (Marzluff et al. 2004). This process produced 4 seasonal population RUF-models for female bison use and 1 non-breeding season model for male bison use. Standardized RUF coefficients can be used to test for population-wide consistency in selection (Marzluff et al. 2004) for individual resources. In accordance with Marzluff et al. (2004) the H_0 that $\overline{\beta_j} = 0$ can be tested by evaluating if the $1 - \alpha$ confidence interval of the population-averaged coefficient contains 0.

RESULTS

Female resource selection

We observed considerable heterogeneity in individual female bison resource selection, although the amount of heterogeneity differed by season (Table 2). We used 23 individual female bison models for the fall, spring, summer, and winter population-level models. The greatest consistency in resource selection occurred during the fall, when only 3 models received support, and the lowest consistency occurred during the spring and summer, when 6 models received support (Table 2). Individual heterogeneity was apparent not only in models that were important to resource selection, but also in the relationship between attributes within models and resource selection. The same resources were both selected and avoided across individuals, which in some seasons resulted in confidence intervals for parameter estimates from the population-averaged model that included 0. Further, heterogeneity existed in mechanisms affecting resource selection across years and seasons, and mechanisms were not consistently important across individuals for a particular year. Out of 23 individuals, only 9 (39%), 4 (17%), 1 (4%), and 7 (30%) individuals were consistent in the mechanism affecting resource selection across years for fall, winter, spring and summer seasons, respectively.

Despite this high amount of heterogeneity, during all seasons three main hypotheses were consistently important to female bison resource selection: habitat type, forage and mineral sites, and water (Table 2). We expected the habitat type model to be supported if bison were selecting resources in a coarse-grained manner. This appears to be the case during the fall and to a lesser extent during the summer and winter (Table 2). For all individuals for which the habitat type model was most supported, there was a consistent avoidance of the fire-killed forest habitat type and selection of the riparian shrubland, mixed-grass prairie, and upland shrubland habitat types. The deciduous forest type was avoided during fall and summer, avoidance of the floodplain woodland during the fall and selection for urban types during the spring. Female bison tended to avoid prairie dog colonies during all seasons, although the 95% confidence interval included 0 for this parameter. Individual bison varied in their responses to the other habitat types.

The remaining hypotheses that received support followed a distinct seasonal pattern. During the winter and spring the forage and mineral sites model was most supported for female bison individuals (Table 2). Female bison selected areas of high warm-season grass biomass during every season except summer, and areas of high forb biomass and close to mineral sites during every season (Table 3). The relationship between female bison resource selection and cool-season grass biomass varied, and was only significant during spring (95 % CI = (10.9, 79.6)), when female biomass selected areas of high cool-season grass biomass (Table 3). Water was most important to bison resource selection during the summer, although it received moderate support during other seasons (Table 2). The relationship between female bison resource selection and water was consistent for every season except spring, and during all seasons, bison selected areas close to ponds and away from streams in CSP (Table 3). Unpredictable disturbance was important to female bison resource selection during the spring season, but received only minimal support during other seasons (Table 2). Female bison selected areas away from unpredictable disturbance and close to visible roads during spring (Table 3). Bison also selected areas away from unpredictable disturbance during the summer and winter, but the relationship was not significant as the 95% confidence intervals for the population-averaged model included 0 (Table 3).

When applied to the landscape, the seasonal population-level RUF models predicted use similarly across CSP (Figure 2) and generally performed well to cross-validation. For all seasons, predicted female bison use was high in the prairie region and low in the forested areas in CSP. However there are differences, the spring and summer RUF models appear to predict use more similarly to each other than to the fall and winter RUF models, and vice versa (Figure 2). In general, predicted areas of high use for female bison were more localized during the fall and winter, and spread more broadly across the study area during spring and summer (Figure 2). Spearman rank correlations between with-held bison locations and predicted probability of occurance indicated the models performed well for fall (r = 0.895), summer (r = 0.868), spring (0.956) and winter (0.840).

Male resource selection.

To estimate population-level seasonal RUF models, we used 7 individual male bison models for the non-breeding model; we did not have a sufficient number of locations to calculate UDs for 3 of the radio-tagged bison males. The amount of heterogeneity we observed in individual male bison resource selection was high. None of the parameters in the population-averaged model were significant due to the high amount of heterogeneity in both models important to male bison selection and in the direction of parameters in those models across individual males (Table 3). The most supported model was forage and mineral sites, which received the most support for only 3 of the 7 individuals (Table 2). However, the relationship between individuals and the parameters in the forage and mineral sites model varied considerably (Table 3). The forage and water model was the most supported model for 2 individuals, and the predictable disturbance, and forage and disturbance models were all most supported for 1 individual each.

There were several differences between male and female bison resource selection in CSP. The relationship of male bison with streams, mineral sites, and cool-season grass biomass was opposite of female bison; male bison selected areas close to streams, away from mineral sites, and negatively associated with cool-season grass biomass (Table 3). However, male bison were similar to females in selection of areas of predictable disturbance density and high warm-season grass and forb biomass, and did select areas of high cool-season biomass when it was located close to water. Males also selected areas away from human disturbance, and cool-season biomass far from disturbance, but close to areas of warm-season biomass near disturbances.

When applied to the landscape, the non-breeding season population-level RUF model predicted high male bison use in the mixed grass prairie and upland shrubland areas of CSP (Figure 3). Overall, the male bison probability of occurrence map appears similar to the spring and summer seasonal female maps (Figures 2 and 3), however, the utility of this map is questionable given the high level of individual variability in parameter values. Given our small sample size, and high individual heterogeneity, is it not surprising that the male population-level model did not predict male use well with the cross-validation (r = 0.05).

DISCUSSION

We found evidence of considerable individual heterogeneity in the mechanisms affecting bison resource selection in CSP, especially during the spring and summer, that has important implications for assumptions regarding resource selection of large gregarious ungulates. Studies of other large ungulates (D'Eon and Serryoua 2005, Gustine et al. 2006, Gillingham and Parker 2008, Dzialak et al. 2011), have reported considerable individual variation in resource selection, and recent literature has highlighted the importance of evaluating individual variation in resource selection studies (Thomas and Taylor 1990, Bolnick et al. 2003, Gilles et al. 2006, McLoughlin et al. 2010). The amount of individual heterogeneity we observed was greater than reported for bison in the Tallgrass Prairie Preserve in Kansas (Allred et al. 2011), a difference that may be due the greater heterogeneity in habitat types in Custer State Park. However, most studies of bison resource selection disregard individual heterogeneity, and bison are assumed to select resources at the herd level rather than the individual level, as individuals in groups tend to synchronize activities (Jarman 1974, Conradt and Roper

2000). Other studies demonstrated that resource selection of bison (Fortin et al. 2009) and other social ungulates (Fritz and De Garine-Wichatitsky 1996) can be dependent upon group size, which we did not evaluate in our study. Our findings highlight the importance of evaluating individual heterogeneity, even with herd animals, as pooling locations across individuals will likely mask the full suite of factors affecting animal resource selection.

We found that bison resource selection in CSP is complex and seasonally dynamic. While bison in CSP may select for areas of high forage biomass in general, similar to bison populations reported elsewhere (Wydeven and Dahlgren 1985, Krueger 1986, Steuter et al. 1995), there was consistent seasonal selection for water sources, mineral sites, and areas away from unpredictable disturbance by female bison groups. This seasonal change in resource selection suggests bison do not forage randomly within the prairie, a finding that has considerable support in the literature (Plumb and Dodd 1993, Steuter et al. 1995, Wallace et al. 1995, Biodini et al. 1999, Schuler et al. 2006, Fortin et al. 2009).

We observed an increase in the importance of the forage and mineral sites model during spring, when lactation begins and when forages are high in potassium (Jones and Hansen 1984, Klaus and Schmidg 1998). Natural or artificial mineral sites have been documented to influence space use of most wild (Risenhoover and Peterson 1986, Ayotte 2004, Watts and Schemnitz 1985, Calef and Lortie 1975, Fraser and Reardon 1980), and domestic (Bailey et al. 2008) ungulates. Wild ungulates may seek out natural mineral licks and supplements because sodium contents of most forage species in North America are low (Jones and Hansen 1984) or to balance toxicity of some plant species (Ayotte et al. 2008). Range scientists have long recognized that mineral supplements can be used as a tool to influence cattle space-use (Ares 1953, Martin and Ward 1973, Ganskopp 2001, Bailey et al. 2008), and our results suggest they could also be used to influence bison grazing patterns. However, because the artificial mineral supplements were undoubtedly placed by park personnel in areas where bison would encounter them, interpretation of bison selection of these mineral sites is not entirely straightforward. Bison in CSP may use areas in close proximity to mineral sites historically for other reasons than the mineral supplement. However, because we included numerous other factors in resource selection models, we are fairly confident that bison are attracted to artificial mineral sites and not some other habitat attribute.

The effect of water on bison distribution is most likely governed by water availability and climate specific to each bison population. Water availability was also important to wood bison (*Bison bison* athabascae) spatial use in Alberta (Mitchell and Gates 2002, Fortin et al. 2003) but not to plains bison (*Bison bison* bison) populations in Utah (Van Vuren 1983, Van Vuren et al. 2001) or Oklahoma (Coppedge and Shaw 1998). In CSP, ponds are more widely distributed in the prairie region while streams are more associated with woody cover. Female bison may prefer ponds as a water source in CSP because streams are associated with higher topographical relief and may be more difficult for large female groups to access or may be associated with a higher risk of predation for juveniles and calves. This hypothesis is supported by the lack of avoidance of streams by bison males, as male ungulates will typically occur in areas of higher predation risk compared to females. Further, female bison avoidance of streams has been documented elsewhere (Allred et al. 2011).

Our results suggest female bison are attracted to areas of predictable disturbances in CSP, which may be due to both habituation to these disturbances and certain features associated with areas of high human activity. Habituation to predictable disturbances has been documented in other ungulate populations and would explain a lack of avoidance to the disturbance (Stankowich 2008), but not a preference for areas of high disturbance. Bison tended to flee from vehicular disturbance in Prince Albert National Park in Canada, but this population experiences much lower amounts of disturbance than the CSP population, and is likely more wary of humans (Fortin and Andruskiw 2003). There are several reasons that bison use may be associated with these areas. Paved roads may simply coincide with areas of high bison activity as they were built to facilitate wildlife viewing for park visitors. Roads have been documented to be important travel routes for bison populations elsewhere (Fortin et al. 2009). Outside of the open prairie region of CSP, primary and secondary roads may provide bison groups with the least strenuous travel corridor into other open areas. Further, some areas associated with human disturbance include campgrounds and building grounds where the grass is mowed during the spring, summer, and fall. Male bison are often observed around campgrounds and park buildings, likely to take advantage of the mowed lawn. These areas likely provide a source of highly nutritious grass, similar to the grazing lawns of the Serengeti (McNaughton 1985).

Although bison appear to not be detrimentally affected by predictable disturbance, they are sensitive to areas of unpredictable disturbance during calving season. Female ungulates with young are typically more sensitive to disturbances than males or females without young (Stankowich 2008), and this type of behavior has also been observed in the bison population in Prince Albert National Park in Canada (Fortin and Andruskiw 2003). Ungulate mothers typically inhabit areas that decrease predation probability of young (Kohlmann et al. 1996, Barten et al. 2001, Grignolio et al. 2007), and because it is believed that ungulates associate human disturbance with predation (Frid and Dill 2002), they also seek areas away from unpredictable human disturbances. Geist (1970) suggested that disturbance that is frequent and unpredictable has the greatest impact on ungulate behavior, and empirical studies have shown this to be true in many wild ungulate populations (Schultz and Bailey 1978, Papouchis et al. 2001, Stankowich 2008). Further, one component of our unpredictable disturbance model was hiking and horse trails. Humans traveling on hiking trails or outside of vehicles tend to illicit greater flight responses from ungulates than vehicular travel (Papouchis et al. 2001, Stankowich 2008). This avoidance of unpredictable disturbances is apparently short-lived, as the model was relatively unimportant to female bison resource selection during summer, when calves are older.

MANAGEMENT IMPLICATIONS

Bison do not forage at random, but instead concentrate use at areas of high quality resources, which in the case of the CSP bison herd, include areas near ponds and artificial mineral sites or areas away from unpredictable disturbance during calving season. Manipulation of water and mineral resources may be an effective tool to manage bison grazing patterns, a method already common practice in cattle management (Bailey et al. 2008). Currently, mineral sites and artificial water sources in CSP are static and are not moved annually or seasonally. Because bison use is high at these areas, we suggest managers consider movement of these sites to influence bison grazing patterns if monitoring indicates these areas are degraded. Bison trampling around water sources can have adverse effects on the vegetative and aquatic invertebrate community (Fritz et al. 1999), thus it may be beneficial to change the locations of these sources. Movement of mineral sites would likely be an easier method to manipulate grazing patterns than removal and reconstruction of water sources, especially since the time required for water sources to be restored may result in a net increase of degraded areas. The movement of mineral sites may induce bison to graze in areas of decadent plant growth, increasing heterogeneity in the landscape. However, bison space use may be less sensitive to changes in water and mineral availability than domestic cattle (Van Vuren 2001), thus it may not be as effective as observed with cattle. Female bison appear to be particularly sensitive to areas of unpredictable disturbance during calving season in CSP. Currently calf survival is considered high in the CSP population (G. Brundige, CSP, personal communication), however if circumstances change in the future managers might consider limiting off-road travel of park personnel and closing hiking trails during the peak of calving season to limit disturbance to females with young.

The probability of occurrence maps we produced will be used to adjust carrying capacity estimates. Instead of making assumptions about bison resource use, these maps will provide empirical estimates of available forage biomass for both male and female bison. However, given the high heterogeneity of resource selection and low sample size of the male bison, this probability of occurrence map should be used with caution when estimating male bison carrying capacity. Given the low sample size, an occupancy, or other, modeling approach may be more appropriate than the RUF technique we used.

LITERATURE CITED

Allred, B. A., S. D. Fuhlendorf, and R. G. Hamilton. 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. Ecosphere 2:1–17.

Andrei, M. A. 2005. The accidental conservationist: William T. Hornaday, the Smithsonian bison expeditions and the US National Zoo. Endeavour 29:109–113.

Ares, R. N. 1953. Better cattle distribution through the use of meal-salt mix. Journal of Range Management 6:341–346.

Ayotte, J. B. 2004. Ecological importance of licks to four ungulate species in north-central British Columbia. Thesis, University of Northern British Columbia, Prince George, British Columbia, Canada.

Ayotte, J. B., Parker, K. L., and M. P. Gillingham. 2008. Use of natural licks by four species of ungulates in northern British Columbia. Journal of Mammalogy 89:1041–1050.

Bailey, D. W., H. C. VanWagoner, R. Weinmeister, and D. Jensen. 2008. Comparison of low-moisture blocks and salt for manipulating grazing patterns of beef cows. Journal of Animal Science 86:1271–1277.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65:77–92.

Belovsky, G. E. and J. B. Slade. 1986. Time budgets of grassland herbivores. Oecologia 70:53–62.

Berger, J., and C. Cunningham. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York, New York, USA.

Biondini, M. E., A. A. Steuter, and R. G. Hamilton. 1999. Bison use of fire-managed remnant prairies. Journal of Range Management 52:454–461.

Bjornlie, D. D., and R. A. Garrott. 2001. Effects of winter road grooming on bison in Yellowstone National Park. Journal of Wildlife Management 65:560–572.

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist 161:1–23.

Brookshier, J. 2000. Effects of forced-weaning on mother daughter associations and reproduction in bison (Bos bison). Thesis, Utah State University, Logan, Utah, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multi-model inference. Springer-Verlag, New York, New York, USA.

Calef, G. W., and G. M. Lortie. 1975. A mineral lick of the barren-ground caribou. Journal of Mammalogy 56:240–242.

Cogan, D., H. Marriott, M. Pucherelli. 2004. Custer State Park, South Dakota, vegetation mapping project. Technical Memorandum 8260-04-01, U. S. Bureau of Reclamation Technical Service Center, Remote Sensing and GIS Group, Denver, Colorado, USA.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258–264.

Coppock, D. L., J. E. Ellis, J. K. Delting, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie: II. Reponses of bison to modification of vegetation by prairie dogs. Oecologia 56:10–15.

Conradt, L., and T. J. Roper. 2000. Activity synchrony and social cohesion: a fission-fusion model. Proceedings of the Royal Society 267:2213–2218.

CSP. 1995. Custer State Park resource management plan 1995–2010. Unpublished document.

D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736–744.

Daleszczyk, K., M. Krasinska, Z. A. Krasinski, and A. N. Brunevich. 2007. Habitat structure, climatic factors, and habitat use by European bison (*Bison bonasus*) in Polish and Belarusian parts of the Bialowieza Forest, Poland. Canadian Journal of Zoology 85:261–272.

Duong, T. 2009. ks: Kernel smoothing. R package version 1.6.8. http://CRAN.R-project.org/package=ks

Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing. 2011. Priotizing conservation of ungulate calving resources in multiple-use landscapes. PLoS ONE 6: [online] e145597.doic10.1371/journal.pone.0014597

Ecological Software Solutions, 2007. LOAS Version 4.0. Ecological Software Solutions, Sacramento, California, USA.

Environmental Systems Research Institute. 2006. ArcGIS: Release 9.2 [software] Redlands, California: Environmental Systems Research Institute, 1999–2006.

Fortin, D. J., and M. Andruskiw. 2003. Behavioral response of free-ranging bison to human disturbance. Wildlife Society Bulletin 31:804–813.

Fortin, D. J., and M. E. Fortin. 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. Animal Behaviour 78:887–892.

Fortin, D J., M. E. Fortin, H. L. Beyer, T. Duchesne, S. Courant, and K. Dancose. 2009. Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. Ecology 90:2480–2490.

Fortin, D, J. M. Fryxell, L. O'Brodovich, and D. Frandsen. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134:219–227.

Fraser, D., and E. Reardon. 1980. Attraction of wild ungulates to mineral-rich springs in central Canada. Holartic Ecology 3:36–40.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6: 11. [online] http://www.consecol.org/vol6/iss1/art11

Fritz, H., and M. De Garine-Wichatitsky. 1996. Foraging in a social antelope: effects of group size on foraging choices and resource perception in impala. Journal of Animal Ecology 65:736–742.

Fritz, K. M., W. K. Dodds, and J. Pontius. 1999. The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. American Midland Naturalist 141:253–265.

Ganskopp, D. 2001. Manipulating cattle distribution with salt and water in large arid-land pastures: a GPS/GIS assessment. Applied Animal Behavioral Science 73:251–262.

Geist, V. 1970. A behavioral approach to the management of wild ungulates. Pages 413-424 *in* E. Duffey and A. S. Watt, editors. Scientific management of animal and plant communities for conservation. Eleventh Symposium of the British Ecological Society. Blackwells Scientific, Oxford, England.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gillingham, M. P., and K. L. Parker. 2008. Differential habitat selection by moose and elk in the Besa-Prophet area of northern British Columbia. Alces 44:41–63.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed kernel analysis of animal range use. Journal of Wildlife Management 70:1334–1344.

Grignoli, S., I. Rossi, E. Bertolotto, B. Bassano, and M. Apollonio. 2007. Influence of the kid on space use and habitat selection of female alpine ibex. Journal of Wildlife Management 71:713–719.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, D. C. Heard. 2006. Interpreting resource selection at different scales for woodland caribou in winter. Journal of Wildlife Management 70:1601–1614.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Devlopment of a 2001 national land cover database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behavior 48:215–266.

Jenness, J. 2010. DEM Surface Tools (surface_area.exe) v.2.0.230. Jenness Enterprises. Available at: http://www.jennessent.com/arcgis/surface_area.htm.

Jones, R. L., and H. C. Hanson. 1984. Mineral licks, geophagy, and biogeochemistry of North American ungulates. Iowa State Press, Ames, Iowa, USA.

Klaus, G, and B. Schmidg. 1998. Geophagy at natural licks and mammal ecology: a review. Mammalia 62:482–498.

Kohlmann, S. G., D. M. Muller, and P. U. Alkon. 1996. Antipredator constraints on lactating Nubian ibexes. Journal of Mammalogy 77:1122–1131.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760–770.

Larter, N. C., and C. C. Gates. 1994. Home-range size of wood bison: effects of age, sex, and forage availability. Journal of Mammalogy 75:142–149.

Loomis, J. 2004. How bison and elk populations impact park visitation: a comparison of results from a survey and a historic visitation regression model. Society and Natural Resources 17:941–949.

Martin, S. C., and D. E. Ward. 1973. Salt and meal-salt help distribute cattle use on semidesert range. Journal of Range Management 26:94–97.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411–1427.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. VanderWal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4–12.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem. Ecological Monographs 55:259–294.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing. Journal of Wildlife Management 64:994–1003.

Mitchell, J., and C. C. Gates. 2002. Status of wood bison (*Bison bison* athabascae) in Alberta. Alberta Sustainable Resource Development and Alberta Conservation Association, Wildlife Status Report No. 38, Edmonton, Alberta, Canada.

Mooring, M. S., D. D. Reisig, E. R. Osborne, A. L. Kanallakan, B. M. Hall, E. W. Schaad, D. S. Wiseman, and R. R. Huber. 2005. Sexual segregation in bison: a test of multiple hypotheses. Behaviour 142:897–927.

Norland, J. E. 1984. Habitat use and distribution of bison in Theodore Roosevelt National Park. Thesis, Montana State University, Bozeman, Montana, USA.

Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. The Journal of Wildlife Management 65:573–582.

Peden, D. G., G. M. Van Dyne, R. W. Rice, and R. M. Hansen. 1973. The trophic ecology of *Bison bison l.* on shortgrass plains. Journal of Applied Ecology 11:489–498.

Pfeiffer, K. E., and D. C. Hartnett. 1995. Bison selectivity and grazing response of little bluestem in tallgrass prairie. Journal of Range Management 48:26–31.

Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3:631–643.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Risenhoover, K. L., and R. O. Peterson. 1986. Mineral licks as a sodium source for Isle Royale moose. Oecologia 71:121–126.

Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293–313.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. 63:739–747.

Schuler, K. L., D. M. Leslie, J. H. Shaw, and E. J. Maichak. 2006. Temporal-spatial distribution of American bison (*Bison bison*) in a tallgrass prairie fire mosaic. Journal of Mammalogy 87:539–544.

Schultz, R. D., and J. A. Bailey. 1978. Responses of National Park elk to human activity. The Journal of Wildlife Management 42:91–100.

Shaw, J. H., and T. S. Carter. 1990. Bison movements in relation to fire and seasonality. Wildlife Society Bulletin 18:426–430.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review. Biological Conservation 141:2159–2173.

Steuter, A. A., E. M. Seinauer, G. L. Hill, P. A. Bowers, L. L.Tieszen. 1995. Distribution and diet of bison and pocket gophers in a Sandhills prairie. Ecological Applications 5:756–766.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322–330.

Van Vuren, D. 1983. Group dynamics and summer home range of bison in southern Utah. Journal of Mammalogy 64:329–332.

Van Vuren, D. 1984. Summer diets of bison and cattle in southern Utah. Journal of Range Management 37:260–261.

Van Vuren, D. 2001. Spatial relations of American bison *Bison bison* and domestic cattle in a montane environment. Animal Biodiversity and Conservation 24:117–124.

Wallace, L. L., M. G. Turner, W. H. Romme, R. V. O'Neil, and Y. Wu. 1995. Scale of heterogeneity of forage production and winter foraging by elk and bison. Landscape Ecology 10:75–83.

Watts, T. J., and S. D. Schemnitz. 1985. Mineral lick use and movement in a remnant desert bighorn sheep population. Journal of Wildlife Management 49:994–996.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.

Wydeven, A. P. and Dahlgren, R. B. 1985. Ungulate habitat relationships in Wind Cave National Park. Journal of Wildlife Management 49:805–813.

Table 1. A priori hypotheses and corresponding models to explain seasonal bison resource selection in Custer State Park, South Dakota, October 2005–August 2008.

Hypothesis	Model
Forage	β_0 + β1(cool-season grass biomass) + β2(warm-season grass biomass) + β3(forb biomass) + β4(shrub patch density[a])
Water	β_0 - β_1(distance to stream[a]) - β_2(distance to pond[a])
Thermoregulation	β_0 + β_1(solar radiation) - β_2(canopy cover[a])
Predator avoidance	β_0 - β_1(terrain ruggedness) + β_2(distance to forest[a])
Total disturbance	β_0 - β_1(total disturbance density[a]) - β_2(visibility)
Predictable disturbance	β_0 - β_1(predictable disturbance density[a]) - β_2(visibility)
Unpredictable disturbance	β_0 - β_1(unpredictable disturbance density[a]) - β_2(visibility)
Forage- water interaction	β_0 - β_1(cool-season grass biomass) - β_2(warm-season grass biomass) + β_3(inverse distance to water) + β_4(cool-season biomass × inverse distance to water) + β_5(warm-season biomass ×inverse distance to water)

Table 1, Continued.

Hypothesis	Model
Forage-disturbance interaction	$\beta_0 - \beta_1$(cool-season grass biomass) - β_2(warm-season grass biomass) + β_3(inverse distance to disturbance) + β_4(cool-season biomass × inverse distance to disturbance) + β_5(warm-season biomass ×inverse distance to disturbance)
Forage and mineral sites	$\beta_0 + \beta_1$(cool-season grass biomass) + β_2(warm-season grass biomass) + $\beta2$(forb biomass) - β_4(distance to mineral site)
Habitat type	$\beta_0 - \beta_1$(barren) - β_2(coniferous forest) - β_3(deciduous forest) - β_4(floodplain woodland) - β_5(urban) + β_6(prairie dog) - β_7(post-fire) - β_8(riparian shrubland) + β_9(grassland) + β_{10}(shrubland) - β_{11}(wetland)
Herd accommodation	$\beta_0 - \beta_1$(terrain ruggedness) + β_2(patch size)

Table 2. Number of times each model of bison resource utilization functions received the most support, and range of Akaike values, at Custer State Park, South Dakota, for fall, winter, spring and summer for female bison and for the nonbreeding season for male bison.

	Fall w_i		Winter w_i		Spring w_i		Summer w_i		Non-breeding season males w_i	
Model	*n*	(Range)	*N*	(Range)	*N*	(Range)	*n*	(Range)	*n*	(Range)
Water	6	0.96 (0.68–1.00)	7	1.00	4	1.00	29	1.00		
Predictable Disturbance			4	1.00			2	1.00	1	1.00
Unpredictable Disturbance			1	1.00	18	1.00 (0.97–1.00)	2	1.00		
Forage and Mineral Sites	7	1.00 (0.97–1.00)	30	1.00 (0.97–1.00)	17	1.00	5	1.00	3	1.00

Table 2, Continued.

	Fall w_i		Winter w_i		Spring w_i		Summer w_i		Non-breeding season males w_i	
Model	*n*	(Range)	*N*	(Range)	*n*	(Range)	*n*	(Range)	*n*	(Range)
Forage and Water			3	1.00	3	1.00			2	1.00
Forage and Total Disturbance			1	1.00	1	1.00			1	1.00
Habitat Type	25	0.99 (0.79–1.00)	11	1.00	13	1.00	17	1.00		

Table 3. Population-level resource utilization functions (β) and standard errors (SE) for bison at Custer State Park, South Dakota, for fall, winter, spring and summer for female bison and for the non-breeding season for male bison.

	Fall		Winter		Spring		Summer		Males non-breeding season	
Parameter	β	SE	β	SE	β	SE	β	SE	β	SE
Intercept	7003.3	244.7	10320.5	545.7	8199.4	386.8	5928.4	136.1	31503.5	12198.5
Distance to stream	160.3	59.6	158.4	67.3	41.1	21.1	275.5	46.8	-129.4	129.4
Distance to pond	-157.6	74.1	-196.3	89.9	-143.9	78.0	-690.2	101.6	-261.9	261.9
Predictable disturbance density			202.6	113.2			52.2	36.6	1677.9	3073.6
Unpredictable disturbance density			-49.5	49.5	-980.0	267.8	-36.8	36.8		
Visibility			7.0	5.7	-60.5	17.0	-2.6	2.0	-176.7	252.0
Cool-season grass biomass	-1.9	9.2	31.6	31.3	45.3	17.2	5.0	4.9	-12.8	549.2

Table 3, Continued.

	Fall		Winter		Spring		Summer		Bulls non-breeding season	
Parameter	β	SE	β	SE	β	SE	β	SE	β	SE
Warm season grass biomass	71.2	30.5	430.0	91.4	137.3	31.7	-2.4	4.3	2020.7	1155.6
Forb biomass	82.1	51.3	313.7	65.8	158.4	77.0	14.8	9.3	2033.7	1897.2
Distance to mineral sites	-250.8	121.1	-1314.6	183.6	-689.6	165.6	-88.7	37.8	2929.9	6287.9
Inverse distance to water			240.2	132.7	68.2	48.5			-353.2	518.0
Cool season grass biomass × inverse distance to water			-47.3	29.4	5.2	7.2			313.6	269.6

Table 3, Continued.

	Fall		Winter		Spring		Summer		Bulls non-breeding season	
Parameter	β	SE	β	SE	β	SE	β	SE	β	SE
Warm season grass biomass × inverse distance to water			-159.6	91.4	-19.3	13.4			-571.2	512.0
Inverse total disturbance density			-3.9	3.9	-0.7	0.7			1216.7	1342.5
Cool season grass biomass × inverse disturbance density			0.1	0.1	0.1	0.1			406.2	298.8
Warm season grass biomass × inverse disturbance density			-0.1	0.1	-0.4	0.4			-2894.7	2103.1

Table 3, Continued.

	Fall		Winter		Spring		Summer		Males non-breeding season	
Parameter	β	SE	β	SE	β	SE	β	SE	β	SE
Coniferous forest[a]	-32.3	34.3	-49.8	45.9	17.4	10.7	1.8	13.8		
Deciduous forest[a]	-31.8	5.6	3.0	6.1	-2.2	1.3	-11.6	3.0		
Floodplain woodland[a]	-33	14.5	-10.2	15.5	-2.4	5.5	-15.4	7.9		
Urban[a]	1.2	11.7	-7.9	11.1	15.2	4.9	-3.2	5.5		
Prairie dog colony[a]	-6.5	8.6	-31.8	15.3	-1.3	2.9	-6.1	3.1		
Post-fire vegetation[a]	-294.8	45.9	-83.3	30.4	-95.7	24.7	-104.9	29.1		

Table 3, Continued.

	Fall		Winter		Spring		Summer		Males non-breeding season	
Parameter	β	SE	β	SE	β	SE	β	SE	β	SE
Riparian shrubland[a]	80.3	12.3	70.6	30.7	30.8	7.3	23.8	6.8		
Upland grassland[a]	522.1	72.6	201.6	61.1	224.7	49.8	153.9	45.3		
Upland shrubland[a]	560.6	77.2	201.6	84.5	177.2	41.1	150.2	37.9		
Wetland herbaceous vegetation[a]	-16.1	12.5	8.7	4.5	4.7	5.3	-1.4	4.7		

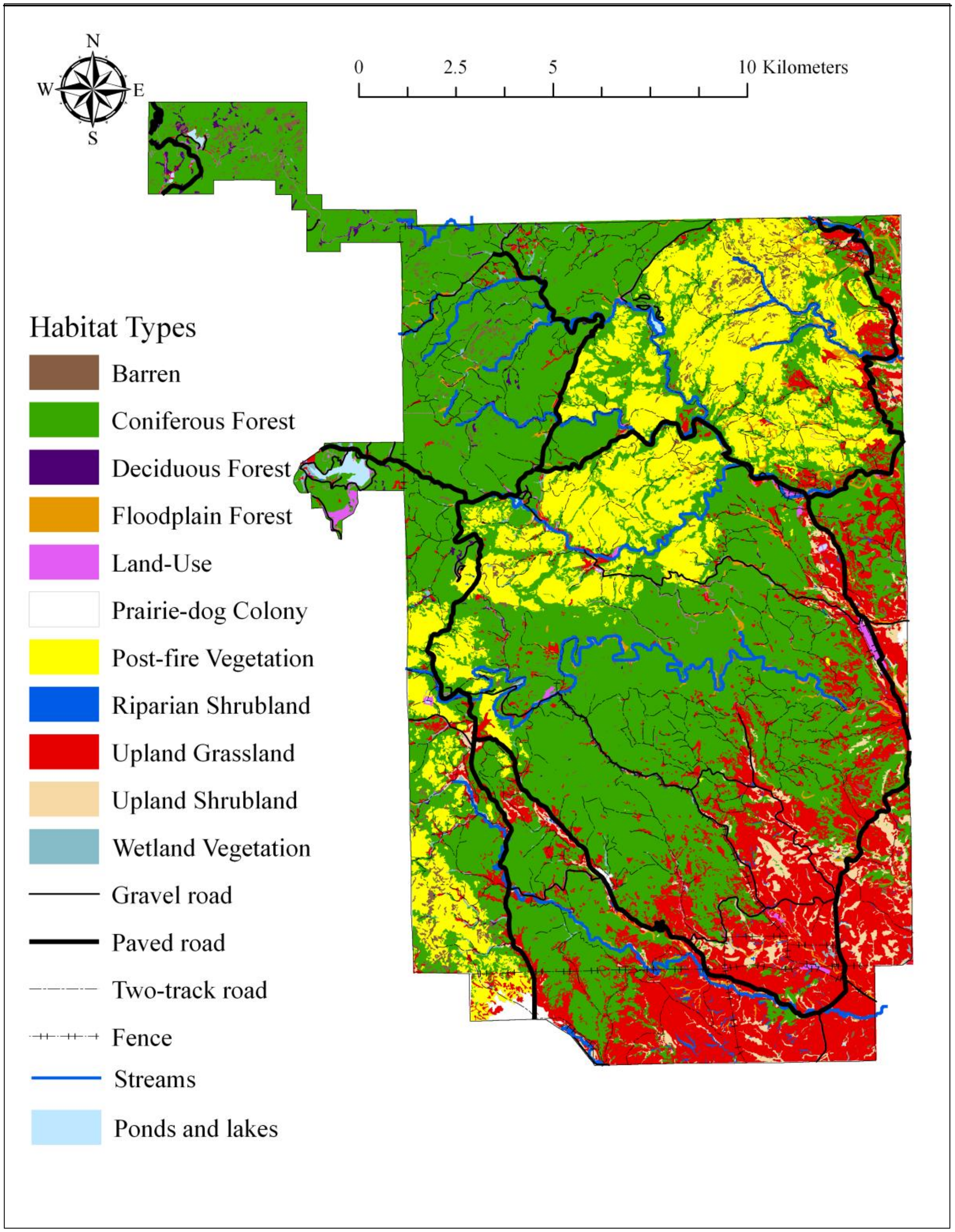

Figure 1. Major habitat types and features of Custer State Park, SD.

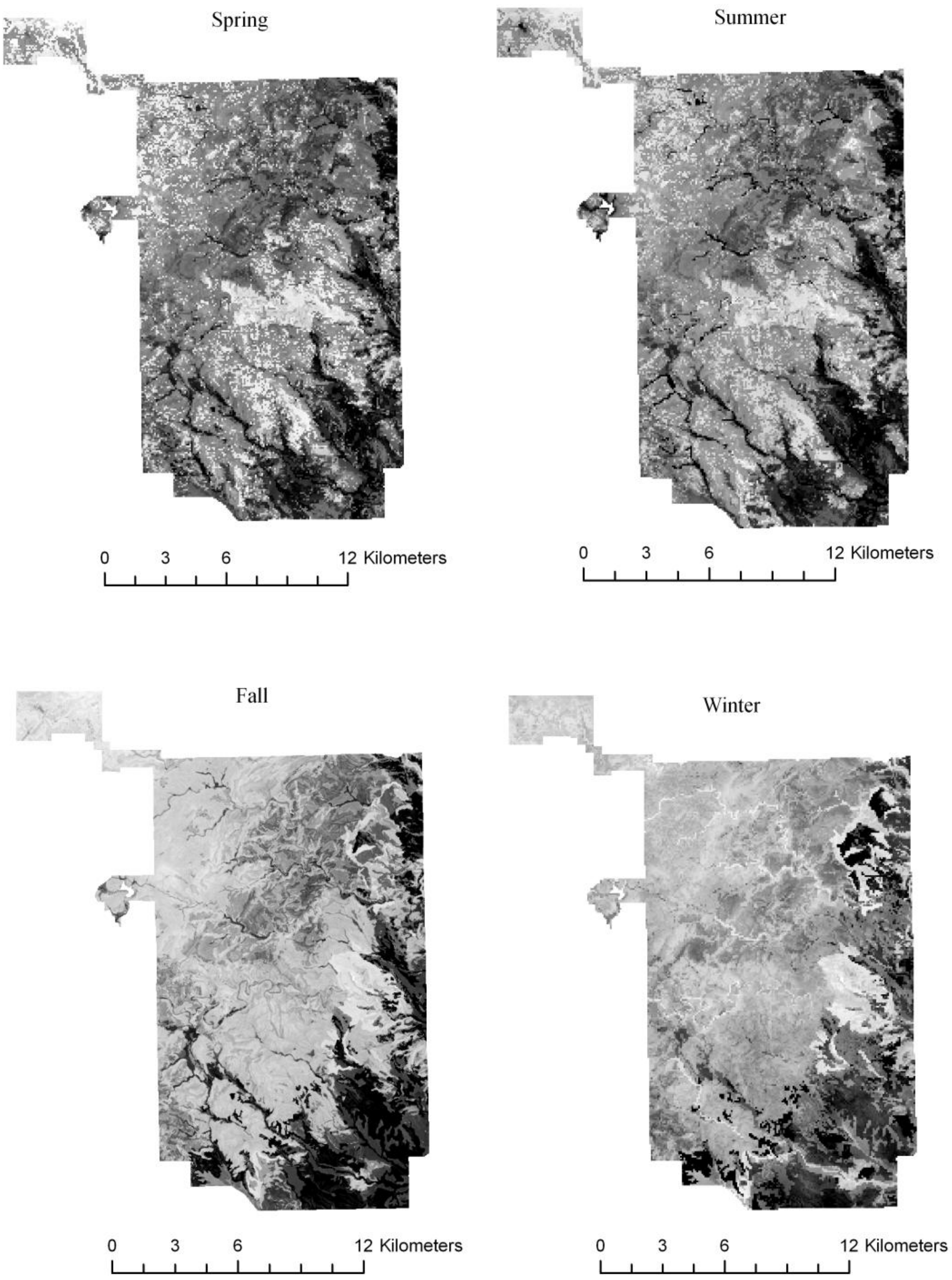

Figure 2. Spatial patterns of predicted selection for female bison during spring, summer, fall and winter in Custer State Park, SD, 2005-2008. Relative probability of occurrence is indicated by gray-scale colors from low (light) to high (dark).

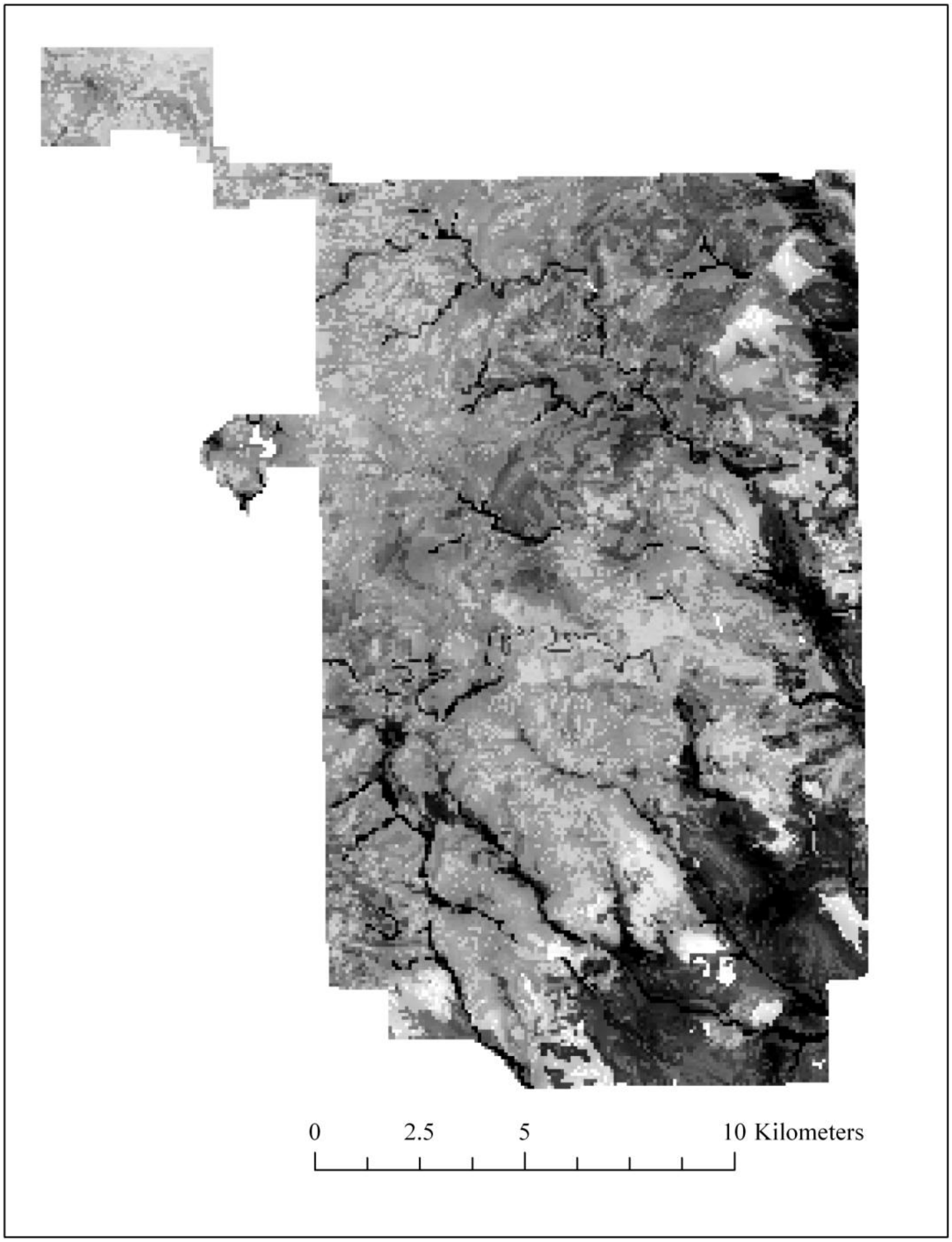

Figure 3. Spatial patterns of predicted selection for male bison during the non-breeding season in Custer State Park, SD, 2005-2008. Relative probability of occurrence is indicated by gray-scale colors from low (light) to high (dark).

CHAPTER III: FACTORS INFLUENCING SEASONAL RESOURCE SELECTION OF PRONGHORN IN THE BLACK HILLS OF SOUTH DAKOTA

ABSTRACT

Management of pronghorn (*Antilocapra americana*), North America's only endemic ungulate species, is complicated by habitat loss, livestock fencing, and energy development throughout much of the species' range. Identification of mechanisms governing resource selection is an important component of species conservation, but few studies have evaluated hypotheses about why pronghorn select different habitats. The pronghorn population in Custer State Park provided a unique opportunity to examine resource selection in an expanding, non-migratory, and non-hunted herd that competes with a full ungulate assemblage. We radio-collared 50 male and female adult pronghorn with 30 collars due to replacement from mortalities, and collected 9,135 locations from November 2005–August 2008. We developed utilization distributions for each individual by season and year, and ranked 12 *a priori* models related to prevailing hypotheses about pronghorn habitat-relationships, based on their ability to account for differential space use within each pronghorn's home range. We combined individual models and developed seasonal population-level resource selection models that we used to predict pronghorn occurrence throughout the Park. Although individual pronghorn varied in their selection of resources, forage, water, areas associated with human disturbance, and combinations of these habitat covariates were consistently important. During most seasons, pronghorn selected areas of high forage biomass close to ponds and far from streams. Pronghorn also reacted to seasonal changes in human disturbance; during the fall and spring pronghorn selected areas of high forb biomass that were close to human disturbance, but during the winter and summer, selected areas of high forb biomass away from human disturbance. Areas of high use during spring and winter were more concentrated than during summer and fall. In general, predicted pronghorn use was highest in the area of Custer State Park occupied by mixed-grass prairie, but also was high in portions of fire-killed forest. Our results support the prevailing hypothesis that forage is the most important factor governing pronghorn resource selection; however, pronghorn seek out foraging areas within the context of unique seasonal stressors, such as human disturbance and water during summer. Thus, management and conservation of pronghorn populations should focus on forage production, but also consider human disturbance and the types of water sources that are available.

INTRODUCTION

Pronghorn (*Antilocapra americana*), North America's only endemic ungulate species, are an valuable and unique component of the western landscape. Typically found in dry, open landscapes of western North America, pronghorn range from the Sonoran and Chihuahuan deserts of northern Mexico to the plains of central Canada (Yoakum 2004). In many of these areas, pronghorn are the last remnant of the Great Plains or western ungulate assemblage. Information on pronghorn resource selection is an important component in their continued conservation, especially as energy extraction, agriculture, and urban development continue to segment remnants of the American west (Yoakum 2004). An understanding of primary mechanisms governing why pronghorn select certain resources would help identify areas of special conservation concern and anticipate the effects of disturbance and development on pronghorn populations.

Factors believed to be important in pronghorn resource selection include forage (primarily forbs and shrubs; Hervert et al. 2005, Boccadori et al. 2008), predator avoidance (Barnowe-Meyer et al. 2010), human disturbance (Fairbanks and Tullous 2002, Gavin and Komers 2006), and water (Hervert et al. 2005, Morgart et al. 2005). However, mechanisms influencing pronghorn resource selection are rarely, if at all, tested empirically. Of the 92 studies that have been published in *The Journal of Wildlife Management* and *The Journal of Mammalogy* concerning pronghorn, only 8 (8.7%) evaluated resource selection of adult pronghorn, and none incorporated information theoretic hypothesis-testing in the analysis (although see example in MacKenzie 2006; Keller, B., University of Missouri, unpublished data). Although pronghorn may use slopes when they are associated with forage (Clary and Beale 1983) or to mediate extreme environmental conditions (Clary and Beale 1983, Bright and Van Riper 2001), it is believed pronghorn utilize flat open areas to facilitate a predator avoidance strategy which uses speed, eyesight, and group foraging behavior to avoid predation (Byers 1997) and for the availability of forage in these areas (Yoakum 2004). However, during and after parturition, pronghorn females and neonates select areas with adequate hiding cover, usually areas of high shrub density (Alldredge et al. 1991, Canon and Bryant 1997, Bright and Van Riper 2001). The relative importance of forage, predator avoidance, or human disturbance to pronghorn resource selection and how these may change on a seasonal basis has not yet been evaluated empirically, to our knowledge.

In South Dakota, pronghorn occupy areas west of the Missouri River, where they typically inhabit broad, open grassland habitat types (Wydeven and Dahlgren 1985, Krueger 1986, Selting and Irby 1997, Bright and Van Riper 2001). Custer State Park, located in the Black Hills of western South Dakota, supports pronghorn in addition to bison (*Bison bison*), elk (*Cervus elaphus*), deer (*Odocoileus virginianus* and *O. hemionus*), bighorn sheep (*Ovis canadensis*), and feral burro (*Equus asinus*) populations. The majority of the pronghorn population remains in a fenced portion of the Park, is not currently hunted and has experienced only light hunting pressure throughout its existence (G. Brundige, Custer State Park, personal communication). The population experienced declines during 2000-2002 but has expanded to roughly 215 individuals (C. Lehman, Custer State Park, unpublished data). Custer State Park provided a unique opportunity to study pronghorn habitat use in an expanding, non-migratory population experiencing mortality that is primarily natural, and at the eastern edge of pronghorn distribution in North America (Yoakum 2004). Our objective was to examine seasonal pronghorn resource selection in CSP. Rather than using an iterative model-building process to develop large descriptive models, we used an information theoretic approach to answer questions about what was driving resource selection of individually-marked pronghorn in CSP; a method by which we can gain more reliable knowledge (Romesburg 1981, Burnham and Anderson 1998) about ungulate ecology. This will be the first study, we are aware of, that tests multiple research hypotheses to address the mechanisms governing pronghorn resource selection.

STUDY AREA

Custer State Park is composed of 286.32 km^2 of rangeland and forest common to the southern Black Hills region in southwestern South Dakota. Steep granite spires characterize the northwest portion of the Park, undulating forested hills interspersed with areas of fire-killed forest dominate the central portion, and grasslands dominate the eastern and southern portions of the Park (CSP 1995; Figure 1). Elevations range from 1,146–2,042 meters (CSP 1995).

The mixed-grass prairie and upland shrubland ecosystem, where pronghorn are typically observed, compose approximately 21% (61.05 km^2) of CSP (CSP 1995; Figure 1). Grasslands are dominated by Kentucky bluegrass (*Poa pratensis*), big bluestem (*Andropogen gerardi*), little bluestem (*Andropogen scoparius*), western wheatgrass (*Agropyron smithi*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*) and sedges (*Carex* spp.; CSP 1995). Dominant shrub species include leadplant (*Amorpha canscens*), western snowberry, wild raspberry, and wild rose (*Rosa* spp.). A 1.54 m woven-wire fence surrounded the majority of the CSP except for a small portion of the Park in the Needles and Sylvan Lake area. This fence prevents movement of bison but allows for movement of all other ungulate species into or out of CSP, although pronghorn do not frequently cross the fence (B. Keller, unpublished data). There are three other internally fenced areas in CSP, which create three distinct pastures in CSP and are used to move bison during the roundup and to manage grazing of bison throughout the year (Figure 1). These internal fences have a 1.33 ft gap above the ground to allow pronghorn movement.

Thirteen watersheds occur either completely or partially within the Park (CSP 1995). There were 6 streams with constant annual flow and numerous ephemeral and permanent water impoundments in CSP during our study period (Figure 1). Water impoundments were created in the prairie region specifically for use by bison and other wildlife, or were already present when CSP was created from old ranching operations. Four large reservoirs exist in CSP, although two of these are outside of the fenced portion of the park and unavailable to pronghorn. The other two reservoirs were located outside of the prairie region. There were two solar-driven water troughs located in the prairie region during the study period that provided a constant supply of fresh water for wildlife.

For 1992–2008, annual precipitation for CSP averaged 49.86 cm and ranged from 74% to 161% of the 25-year mean. Approximately 76% of precipitation in CSP fell from April to September (unpublished data). Winter in the southern Black Hills is considerably more mild than elsewhere in the region, and a persistent snowpack was not typically present during the study period. Average snowfall for the southern Black Hills is 32.0 cm; March is the snowiest month with an average snowfall of 18.8 cm. Temperatures in CSP are more moderate than the surrounding plains; the average annual, summer and winter temperature in CSP is 6.7° C, 16° C, and –5° C, respectively (CSP 1995).

Approximately 800–1000 adult bison, 408–718 elk, 163–279 pronghorn, 867 white-tailed deer, 285 mule deer, 38–48 bighorn sheep, and 35–40 feral burros occupied CSP during our study period (C. Lehman, Custer State Park, personal communication). Bison were culled annually during the fall bison roundup, as well as during several hunts during the fall. Coyotes (*Canis latrans*), mountain lions (*Felis concolor*) and bobcats (*Felis rufus*) were the major predators in CSP.

METHODS

Capture and monitoring

We used a handheld netgun to capture pronghorn from a vehicle along roads throughout the prairie region of CSP (Figure 1). Pronghorn typically reside in open grasslands that allowed us to locate groups of pronghorn from a distance. We were able to approach to within 6 m of pronghorn on roads in CSP because this population was accustomed to a high level of vehicular disturbance. We also traveled off-road in the vehicle to capture pronghorn, although the paved, gravel and two-track roads covered much of pronghorn territory in CSP (Figure 1). We manually restrained and fitted each netted pronghorn with a mortality sensing radio-collar (Advanced Telemetry Systems, Isanti, MN, USA) We aged pronghorn according to incisor irruption and tooth wear (Dow and Wright 1962). We attempted to maintain an equal distribution of collars among both sexes by tagging animals during each capture based on the sex of pronghorn mortalities the previous season.

We located pronghorn approximately 5 times per week, based on a rotating schedule that coincided with sunrise and sunset, October 2005 – August 2008. We separated locations by 25–30 hour intervals, and visually confirmed locations or used triangulation techniques during night sampling periods or when weather conditions did not permit off-road travel. We were able to visually confirm 62% of pronghorn locations. Universal Transverse Mercator (UTM) coordinates of collared animals were recorded with a handheld GPS. We only recorded azimuths for triangulation that were < 20 min apart to account for animal movement, and obtained at least 2 azimuths > 45° apart. Telemetry accuracy was evaluated by Millspaugh et al. (2000) for elk in CSP, and mean distance from estimated to true location was 176.1 m (range = 13.4–746.6 m). We used the computer program Location Of A Signal (LOAS; version 4.0, Ecological Software Solutions, 2007) to estimate animal locations from two or more azimuths.

Resource selection hypotheses

We evaluated 12 *a priori* models for each individual pronghorn (Table 1), representing hypotheses based on the literature regarding pronghorn resource selection. We included non-linear forms (pseudo-threshold) of explanatory variables when appropriate.

Forage. Pronghorn alter their seasonal dietary shifts based on forage availability and quality (Salwassar 1980), but generally forage on shrubs and forbs when available (Yoakum 2004). We predicted that pronghorn would select areas of high forb biomass during the spring and summer and shift to areas of high shrub patch density during the fall and winter, and that cool- and warm-season grasses would be relatively unimportant to pronghorn resource selection (Table 1). We used the forage biomass model developed in Chapter 1 to build GIS covariate layers of biomass of cool-season grasses, warm-season grasses, and forbs throughout CSP. The forage biomass model included parameters for range/woodland grazable site, slope, elevation, canopy cover, prairie dog (*Cynomys ludovicianus*) colony, current annual spring precipitation, previous year spring precipitation, and ordinal date of last spring frost. We used the 25-year mean (1983-2008) for spring precipitation variables and the mean ordinal date of last spring frost for 2004-2008. We used Spatial Analyst in ArcGIS 9.2 (Environmental Systems Research

Institute 2006) to estimate shrub patch density in CSP based on a vegetation classification map developed by Cogan et al. (2004).

Water. Pronghorn often meet water needs through preformed water content of forages, and do not need to visit free-standing water sources (Yoakum 2004, Beale and Smith 1970). However, the ability of pronghorn to meet water requirements can change based on the seasonal water content of forages, and can be compromised during drought periods and during the winter (Schwartz et al. 1977). Therefore, we predicted that pronghorn would select areas close to water in CSP, but that selection would change seasonally with greater use during the summer and less use during the winter. The water model consisted of 2 separate parameters, distance from flowing stream, and distance from pond, calculated using Spatial Analyst in ArcGIS 9.2. Coverage of water features were obtained from Cogan et al. (2004).

Forage and water. Because both forage and water are assumed important to ungulates, we created a model considering both forage production and distance to water, and the interaction between these variables. We considered distance to all water in general (combined ponds and streams GIS layers) and calculated its inverse to account for the relative closeness of any pixel to a water site. We multiplied the forb biomass and shrub patch density layers by the inverse water distance layer to create ‘forb production adjusted by distance to water’ and ‘shrub density adjusted by distance to water’ layers. These layers consisted of high values when both forage availability and closeness to water were high, and low values when either forage availability or closeness to water were low.

Human-related disturbance. From 2005–2008, an average of 1,631,432 people visited CSP annually (C. Pugsley, Custer State Park, personal communication) so it is likely that public visitation is the major source of disturbance in CSP. Therefore we modeled disturbances using features related to human visitation, such as roads and campgrounds. Habituation of wildlife to certain predictable human disturbances is well-documented (Bejeder et al. 2006, Baudainis and Lloyd 2007, Haskell and Ballard 2008). Thus, we hypothesized that the response of pronghorn to human disturbance depended on its predictability and thus separated our human disturbance hypothesis into predictable, unpredictable and total human disturbance subhypotheses. Because public visitation of the park is highly seasonally dependent, pronghorn may have become less habituated to use of certain road types during different seasons. Paved, gravel and two-track roads all occur in CSP (Figure 1). Paved roads were highly traveled during all seasons as three of the paved roads are federal or state highways. Thus, we classified these areas, along with areas of human activity (e.g., buildings and campgrounds) as having predictable disturbance for every season. We assumed trails and two-track roads that were used by park personnel only acted as areas of unpredictable human disturbance during all seasons. However, we hypothesized that the predictability of disturbance on gravel roads varied with season, where the higher occurrence of tourists during spring and summer resulted in more predictable disturbance as compared to fall and winter where gravel roads acted as areas of unpredictable human disturbance. We computed densities of human disturbance features to characterize their presence throughout the park. Because density did not account for topographical or vegetative buffering from roads, we included a "visibility" metric in an alternative submodel to all sub-hypotheses. This visibility metric measured the probability that an animal could be viewed from the road based on topographical features and vegetation structure (G. Roloff, Michigan State University, personal communication).

Forage and human-related disturbance. The forage and human-related disturbance hypothesis accounts for the potential of pronghorn to avoid areas of high forage biomass close to areas of human-related disturbance. We used the total human disturbance density layer (described above) and calculated an inverse total human disturbance density. We multiplied the forb biomass and shrub density layers by the inverse human disturbance density layer to create ‘forb production adjusted by disturbance’ and ‘shrub density adjusted by disturbance’ layers. These layers consisted of high values when both forage availability and human disturbance density were low, and low values when either forage availability or disturbance density were high.

Forage and distance to mineral sites. Natural and artificial mineral sites are areas of high use by wild (Jones and Hanson 1984) and domestic (Bailey et al. 2008) ungulates, but little information is available regarding pronghorn and mineral sites (Yoakum 2004). During our study, park personnel maintained 10 mineral sites in CSP. These mineral sites were replenished with granular mineral several times throughout a year and consisted of a mixture of calcium, phosphorus, salt, magnesium, copper, manganese, zinc, vitamin A, vitamin D, and Vitamin E (Hubbard Feeds Inc., Mankato, Minnesota). Because we predicted pronghorn would select areas in close proximity to mineral sites, we included a distance to mineral site variable in the original forage model to determine if mineral sites were important to pronghorn selection (Table 1).

Thermal Cover and Heat Avoidance. Pronghorn might seek areas to ameliorate seasonal climatic extremes. During winter, pronghorn may select areas where wind speed and chill factors are reduced (Rouse 1959). During the summer, pronghorn may select areas of low solar radiation that provides shade (Hughes and Smith 1990). Although depth has been reported as important in other pronghorn populations (Guenzel 1986), CSP does not experience heavy snowfall during winter. We hypothesized pronghorn would select areas of low solar radiation and high canopy cover during the spring and summer, and high solar radiation and low canopy cover during the fall and winter. We obtained canopy cover from the National Land Cover Database (Homer et al. 2004). Solar radiation was calculated from the digital elevation model (DEM) using the Area Solar Radiation tool in ArcGIS 9.2. This tool uses variation in elevation, slope, aspect, shadows cast by topographic features, and variation in day and time of year to calculate insolation (Environmental Systems Research Institute 2006). We computed solar radiation separately for each season to account for differences due to day length.

Predator Avoidance. The native predator community in CSP consisted of grizzly bears (*Ursus arctos horriblis*), wolves (*Canis lupus*), mountain lions, bobcats, coyotes, and golden eagles (*Aquila chrysaetos*). Grizzly bear and wolves are extirpated from CSP, but populations of all other predators remain. Pronghorn rely on excellent eyesight and running speed to detect and avoid predators (Byers 1997), thus we hypothesized that the ability of pronghorn to detect and avoid predators in CSP would be highest in flat grassland areas. Areas of rugged terrain are associated with predator presence and hiding cover in CSP, and affect the ability of pronghorn to detect and quickly evade predators. Because we predicted pronghorn would select areas of low terrain ruggedness and far from forested cover to avoid predators, our predator avoidance model included terrain ruggedness and distance to forest variables. Terrain ruggedness was represented by a surface ratio value, that we calculated with DEM Surface Tools extension for ArcGIS (Jenness 2010). Surface ratio was calculated as the ratio of surface area to planimetric area in a pixel from the digital elevation model. This ratio is an indicator of topographic roughness (Jenness 2010). Distance to forest was calculated using forest polygons derived from the Cogan et al. (2004) vegetation coverage database.

Habitat Type. We included a habitat type model to account for coarse-grained selection by pronghorn in CSP (Table 1). Pronghorn selection of open grassland habitat (Yoakum 2004) and prairie dog towns (Krueger 1986) has been documented elsewhere. We used the vegetation classification map developed by Cogan et al. (2004) to divide the study area into 11 distinct habitat types: barren, coniferous forest, deciduous forest, floodplain woodland, urban, prairie-dog colony, post-fire vegetation, riparian shrubland, upland grassland, upland shrubland, and wetland herbaceous vegetation. This habitat type raster was used as a categorical explanatory variable in the model. We hypothesized that pronghorn would select upland grassland, upland shrubland, wetlands, and prairie dog towns, but that pronghorn use would be negatively associated with all other habitat types.

Data analysis

To test if our sample was biased to pronghorn that used areas close to roads, we used a Mann-Whitney test of median distance to roads between the 9135 pronghorn locations and 9135 randomly located points within the prairie habitat ($\alpha = 0.05$).

Utilization Distributions and Resource Utilization Functions. We calculated utilization distributions (UD; Worton 1987) for each individual pronghorn for each season and year. We used the KernSmooth package (Duong 2009) in R (R Development Core Team 2009) to develop fixed-kernel UDs, and used the plug-in option for bandwidth estimation that allows for separate smoothing in *x* and *y* directions (Gitzen et al. 2006). We separated locations for each pronghorn into year and season combinations (fall = 1 September – 30 November ; winter = 1 December – 28 February; spring = 1 March – 30 May; summer = 1 June – 30 August). Only pronghorn with ≥ 30 locations for each year-season combination were included in the analysis (Seaman et al. 1999). To combine relative use with habitat attribute data, we imported UDs for each individual into a Geographic Information System (GIS). We defined resource availability for the animal as 95% of the UD boundary, leaving a 95% probability distribution for the animal (Marzluff et al. 2004) and excluded any portion of the UD that fell outside of the CSP park boundary, due to smoothing.

We used resource utilization functions (RUF; Marzluff et al. 2004) to evaluate resource selection of individual pronghorn in CSP. A RUF is similar to a resource selection function (Manly et al. 2002) but uses a continuous measure of resource use (the UD height) rather than a binary measure (used or unused) based on animal locations. We combined resource attributes (variables) into models that represented hypotheses about the mechanisms driving pronghorn resource selection. We ranked these hypotheses by the relative support they had, based on Akaike's information criterion (AIC), to describe the variation in relative use that occurred within each individual's home range.

We used the RUF package in R created by Marzluff et al. (2004; available at www.csde.washington.edu/~handcock/ruf/) to fit the models. We used the ruf.fit function to relate the continuous measure of UD height for each individual to the explanatory variables included in each model. The RUF package fits a regression to each animal's UD with spatial correlation as a function of the distance between the pixels, using a stationary model from the Matern class that is function of the Euclidian distance between two locations (Marzluff et al. 2004). In our case, the distance between locations corresponded to the bandwidth used to estimate each individual's UD. We calculated standardized coefficients for each model (see below).

Model Selection. We used AIC to ranks models for each individual animal UD, and used model averaging techniques (Burnham and Anderson 1998) when uncertainty occurred among models (> 1 model accounted for 90% of total Akaike weights). We examined the standardized RUF coefficients from the most supported model for each pronghorn to compare use of resources among seasons and sex-class. The standardized RUF coefficients are calculated as:

$$\widehat{\beta_j} = \hat{\beta}_j^{*} \frac{S_{xj}}{s_{\mathbf{RUF}}}$$

where $\hat{\beta}_j^{*}$ is the maximum likelihood estimate of $\widehat{\beta_j}$, the partial regression coefficient from the multiple regression equation; S_{xj} is the standard deviation of the values of resource *j*; and the $s_{\mathbf{RUF}}$ is the estimate of the standard deviation of the UD heights (Marzluff et al. 2004). Standardized coefficients allow comparisons of the relative influence of resources on pronghorn habitat use (Marzluff et al. 2004). For each individual, we averaged standardized RUF coefficients for the most supported model among years for each season. We estimated a population-level RUF model for each season by averaging the standardized RUF coefficients for the across-year model for each individual (Marzluff et al. 2004). We used a Wald's test to determine if male and female pronghorn population-averaged RUF coefficients significantly differed from each other, if there was no significant difference we pooled male and female models for the population-averaged model. This process produced 4 seasonal population RUF-models for pronghorn use.

Model Validation. We used k-fold cross-validation to validate the seasonal resource selection models (Boyce et al. 2002). First, we randomly selected 20% of the individual pronghorn models from each seasonal population model for 3 folds. Each fold consisted of a testing (the removed 20%) and training (the remaining 80% of models) groups. Second, we recalculated the population-level standardized RUF coefficients for the training group and projected this model on the landscape. Third, we reclassified the study area into 9 bins based on the quantiles of the resulting RUF estimates projected on the landscape. We then projected the locations associated with the withheld individuals on the landscape and RUF model, and tallied the number of pronghorn locations that fell into each of the 9 bins for each fold. We used a Spearman-rank correlation to observe the relationship between area-adjusted frequencies of locations and RSF bins; a strong correlation (≥ 0.70) was indicative of a good model (Boyce et al. 2002). We averaged the Spearman-rank correlation coefficients among the 3 folds for each season.

RESULTS

We believe the pronghorn spatial use we recorded in CSP adequately represented the population. We monitored 50 individual pronghorn (26 males [M], 24 females [F]) with 30 transmitters (due to replacement of collars from mortalities) from November

2005–August 2008. Based on the Wald's test, random points were significantly further from paved and gravel roads than pronghorn locations (W = 68223691, P < 0.0001). However, pronghorn were located a median of 36 m closer to roads than the random points, which is not likely a biologically significant value. We do not think this small difference implies that our sample is not representative of the CSP pronghorn population.

Male and female population-level standardized RUF coefficients did not significantly differ for winter (W = 99.5, P = 0.945), spring (W = 412.5, P = 0.175), summer (W = 142, P = 0.527), or fall (W = 164, P = 0.717). Thus, we pooled male and female RUF models for each season. To estimate population-level seasonal RUF models, we used 26 (13 F, 13 M) individual pronghorn models for fall season (each individual was represented by 1 model), 41 (21 F, 20 M) individual pronghorn models for the spring model, 34 individual pronghorn models for the summer model (21 M, 13 F), and 28 individual pronghorn models for the winter model (13 M, 15 F).

There was considerable individual heterogeneity in factors that were important in resource selection (Table 2); 11 models representing 7 hypotheses were supported among all individuals and seasons. The greatest individual heterogeneity occurred during spring, when 9 models received support, and the lowest heterogeneity occurred during winter, when only 5 models received support to explain individual resource selection (Table 2). Individual heterogeneity was considerable not only in models that were important to resource selection, but also in the relationship between attributes within models and resource selection. For the pooled population model, heterogeneity was so large that most 95% confidence intervals of the population model parameters contained 0. This result implies high variability in individual selection patterns. However there were several exceptions; in spring, there was a significant avoidance of cool-season grass biomass (Table 2), during fall there was agreement in avoidance of streams and selection for areas near ponds, and during winter there was significant selection of forb and shrub biomass, ponds, mineral sites, and areas of high forage biomass close to predictable human disturbances (Table 2).

During all seasons three main hypotheses were consistently important: forage, water, and human disturbance (Table 2). The most important driver of pronghorn resource selection was forb and shrub biomass, but the relationship was strongest when considering biomass in the context of other important seasonal factors, such as human disturbance and proximity to water and mineral sites. When the combination of forage and water and forage and human disturbance models were most supported for pronghorn individuals, pronghorn nearly always selected areas of high forb biomass and shrub patch density, but because the interactions between forage and water and forage and human disturbance were highly variable across pronghorn, this caused standard errors for those population-averaged parameters to be large (Table 3). It was rare that a pronghorn was negatively associated with both forb and shrub biomass without a subsequent positive interaction between forage and human disturbance or water; only 1 individual in spring and 1 individual in fall avoided high forage biomass altogether. In general, during most seasons, pronghorn selected areas of high forb biomass that were far from water, except for spring, when pronghorn selected areas of high forb biomass close to water (Table 3). During winter and spring pronghorn selected areas of high forb biomass that were close to human disturbance on average, but during the fall and summer, selected areas of high forb biomass far from human disturbance (Table 3). Pronghorn selected areas of high shrub patch density near human disturbances during all seasons except fall (Table 3). Pronghorn selected areas of high shrub patch density close to water during the spring and winter and away from water during the summer and fall. Pronghorn selected areas of in close proximity to mineral sites during all seasons (Table 3).

Pronghorn associations with disturbance and water features not only depended on the nature of the human-related disturbance and the type of water features in CSP but also on season. Pronghorn selected areas far from streams and close to ponds during every season except spring, when the reverse occurred (Table 3). Pronghorn also reacted differently to predictable and unpredictable disturbance density. For example, areas of high unpredictable disturbance density, such as trails and two-track roads, were avoided by pronghorn during all seasons. Rather, pronghorn selected areas of high predictable disturbance density during fall and spring, and low predictable disturbance density during the summer (Table 3). Pronghorn showed increased selection for areas with high road visibility except during fall.

Despite the high individual heterogeneity, the cross-validations for most seasons performed well; the summer, winter, and spring seasonal resource selection models averaged Spearman-rank correlations of 0.77, 0.95, and 0.93, respectively. The fall model, however, did not perform well in the cross-validation, with an average Spearman rank correlation of -0.30. The heterogeneity was likely too high, and our sample size of collared individuals too small to adequately capture the average population response to resources for the fall. The success of the cross-validations during most seasons suggest the population averaged model parameters were adequate at predicting pronghorn use, and sufficiently represent the average response of CSP pronghorn to habitat attributes.

When applied to the landscape, the seasonal population-level models predicted areas of high use during the spring and winter that appear much more localized than during the summer and fall, when areas of high predicted pronghorn use are spread over a much broader area (Figure 2). In general, predicted pronghorn use in CSP is highest in the area occupied by mixed-grass prairie and upland shrubland, but is also high in portions of fire-killed forest (Figure 2).

DISCUSSION

Although the degree of individual heterogeneity in pronghorn resource selection we observed was surprising, differences in the number of mechanisms influencing pronghorn resource selection coincided with the seasonal natural history of pronghorn. During winter, pronghorn congregate in large groups and use similar resources, thus this was the period of lowest heterogeneity in individual pronghorn resource selection models and the most agreement of parameter values across individual models. Conversely, during spring and summer, when pronghorn establish territorial home ranges, individual heterogeneity in resource selection was high. This seasonal phenomenon also was apparent with the population models projected on the landscape; the predicted area occupied by pronghorn expanded and contracted throughout the year based on this cycle. Studies of other large ungulates (D'Eon and Serryoua 2005, Gustine et al. 2006, Gillingham and Parker 2008, Dzialak et al. 2011), have also reported considerable amounts of individual heterogeneity in resource selection. Further, similar seasonal changes in the mechanisms influencing ungulate resource selection and spatial distribution of ungulates has been widely reported (Ager et al. 2003, Boyce et al. 2003, D'Eon and Serrouya 2005, Baasch et al. 2010, Stewart et al. 2010).

While it is clear that pronghorn in CSP selected areas with high forage biomass, their association with other resources, such as water and disturbance, was highly variable, and in general, contradicted our predictions. This result may have been driven by particular features and mechanisms not captured in the models. Pronghorn avoidance of certain water types was apparent with the direction of parameter coefficients in the water and the forage and water models. Pronghorn might avoid water due to increased levels of stalking cover for predators at streams, and the rugged topography associated with streams in CSP. The rugged topography and broken terrain might make water difficult for pronghorn to access and was likely associated with a higher risk of predation. These natural breaks in the landscape also might define the edges of territorial home ranges for pronghorn. Furthermore, streams in CSP are associated with high biomass of cool-season grasses and forbs (B. Keller, University of Missouri, unpublished data), forage types that were avoided by pronghorn during certain seasons. Because we combined stream and pond features together in the forage and water hypothesis model, the avoidance of streams by pronghorn in CSP likely produced the result of a negative association between pronghorn selection and forb biomass close to water features, and the variation of pronghorn's responses to water may be driven by the topographic characteristics and forage associated with the water sources within their individual home ranges.

The unexpected selection of pronghorn for areas near disturbances may be due to similar issues with grouping of disturbance features, especially given that pronghorn in CSP apparently react differently to predictable and unpredictable human-related disturbances, and respond to seasonal changes in levels of disturbances. We expected that pronghorn would avoid foraging near human disturbance, which was indeed the case with forb biomass during the summer and fall. There are two possibilities to explain why pronghorn foraged close to human disturbances during the spring and winter. First, pronghorn may react to high levels of human disturbance in CSP that are absent during the spring and winter compared to the summer and fall, when the majority of human visitation in CSP occurs. Although human visitation tends to taper off during the fall, visitor-targeted activities such as the bison roundup and Buffalo Roundup Arts Festival draw over 14,000 visitors to the Park during this time (C. Pugsley, Custer State Park, personal communication). Second, because we combined predictable and unpredictable disturbances in the forage and human-related disturbance model, the differential selection for areas surrounded by predictable and unpredictable disturbances likely confounded the relationship between forage and human disturbance in the model. Avoidance of pronghorn for recreational trails, a component of unpredictable disturbance in our models, has also been observed by Fairbanks and Tullous (2002) for pronghorn in Utah. Unpredictable disturbances (people on foot) have been documented to elicit greater responses in both mule deer (Freddy et al. 1986) and bighorn sheep (MacArthur et al. 1982) than predictable (snowmobiles and vehicles) disturbances. Conversely, other studies have indicated that hunted pronghorn populations avoid or are affected by heavily-traveled roads (Berger et al. 1983, Gavin and Komers 2006, Kolar 2009). Gavin and Komers (2006) suggest that hunted pronghorn may perceive even frequent, predictable disturbances as predation risk if hunters use roads to access pronghorn. Because the CSP pronghorn population is not hunted, pronghorn may not associate roads with predation risk and thus only avoid them during the extreme periods of disturbance that occurs during the summer and fall. Our results suggest that while pronghorn resource selection is negatively associated with unpredictable human-related disturbance, pronghorn will use areas of both predictable and unpredictable disturbances if they coincide with high forage (particularly shrub) biomass.

An alternate explanation for our unexpected results is related to the diverse ungulate assemblage in CSP. It is possible that the high species diversity and relatively high densities of ungulates in the system drove pronghorn to seek forage in areas that were avoided by other ungulates, or pushed pronghorn into undesirable habitats. Pronghorn may have selected areas close to disturbances during the winter and far from water because these were areas that other ungulates in CSP avoided, and as a result there may have been a higher forage biomass in these areas. Pronghorn are not likely to compete with all of the ungulates in CSP given the separation of diets, but do have similar diet selection to mule deer and white-tailed deer during some seasons (B. Keller, University of Missouri, unpublished data). White-tailed deer and mule deer in CSP are located close to water sources during both summer and winter, and elk avoid secondary roads during summer and winter (Woeck 2003). If deer in CSP are more sensitive to disturbance and water needs, pronghorn may seek out forage in these areas avoided by deer. Conversely, if other ungulates behave antagonistically toward pronghorn around preferred water sources, this may lead to an avoidance of those areas by pronghorn.

Despite the avoidance of pronghorn for water features when streams and ponds were combined in the forage and water hypothesis, it was clear that pronghorn selected areas near ponds when the water hypothesis was supported. Although pronghorn may not need to drink freestanding water when moisture content of forages is adequate (Beale and Smith 1970) we found ponds can be important to pronghorn; this conclusion has been reached elsewhere (Clemente et al. 1995, Mogart et al. 2005). Given the possibility that predator avoidance influences pronghorn use of water resources, as indicated above, we could expect pronghorn to select ponds while avoiding streams in CSP. Ponds located in the open prairie lack both the rugged topography and hiding cover associated with streams. This reduction in vegetation, and subsequently stalking cover for predators, may decrease the risk of predation associated with other water sources such as streams in CSP.

Given our hypotheses regarding why pronghorn may avoid streams in CSP, we must address why the predator avoidance hypothesis received very little support for seasonal pronghorn resource selection. Pronghorn in CSP share habitat with numerous predators, including mountain lions, coyotes, bobcats, and golden eagles. Predator avoidance may not be important to pronghorn resource selection because mountain lions have only recently increased in abundance and density in the Black Hills (SDGFP 2005), because pronghorn may not be adapted to escape these types of predators in this habitat, or because we did not include adequate terms in our predator avoidance model. Pronghorn evolved to escape predators most efficiently on flat open terrain (Byers 1997), thus the rolling hills of CSP may not provide the most ideal landscape for pronghorn to escape attacks from mountain lions and coyotes. Further, we observed several pronghorn carcasses in dry stream beds during our study, which may indicate that predators are using cover and broken terrain associated with streams to kill pronghorn; thus, we do not think predator avoidance should be discounted as an important factor in pronghorn resource selection. In future analyses, researchers may want to consider including water sources in models representing predator avoidance.

MANAGEMENT IMPLICATIONS

Our analysis approach allowed us to build predictive models while concurrently testing hypotheses about the mechanisms governing pronghorn resource selection. Research and funding in the field of ungulate ecology is often driven by management agencies. This relationship often results in over-built descriptive models that may adequately address management questions, but might not advance our understanding of mechanistic factors affecting populations. Hypothesis testing is the primary means by which we gain reliable knowledge in wildlife science (Romesburg 1981, Nudds and Morrison 1991). We demonstrated how researchers can build predictive models that generally perform well, while also testing mechanistic hypotheses. Further, we measured resource selection at the individual level; which allowed us to assess variability in resource use within the population. Individual variation is often disregarded in resource selection studies (Thomas and Taylor 1990, Gilles et al. 2006, McLoughlin et al. 2010), since locations are generally pooled across individuals to develop population-level models, which will likely mask the full suite of factors affecting animal resource selection.

Our results supported the prevailing theory that forage is the most important factor governing pronghorn resource selection, but that pronghorn seek out areas supporting high amounts of forage within the context of unique seasonal stressors, such as disturbance during times of peak human visitation and water during the summer. The forage-only hypothesis received very little support in any season to explain pronghorn resource selection. Thus, management and conservation of pronghorn populations should focus not only on forage quantity and quality, but also consider human disturbance and the types of water sources that are available, as pronghorn selected areas near ponds and avoided streams in CSP.

LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. Journal of Mammalogy 84:1076–1088.

Alldredge, A. W., R. B. Deblinger and J. Peterson. 1991. Birth and fawn bed site selection in sagebrush-steppe community. Journal of Wildlife Management 55:222–227.

Baasch, D. M., J. W. Fischer, S. E. Hygnstrom, K. C. VerCauteren, A. J. Tyre, J. J. Millspaugh, J. W. Merchant, and J. D. Volesky. 2010. Resource selection by elk in an agro-forested landscape of northwestern Nebraska. Environmental Management 46:725–737.

Bailey, D. W., H. C. VanWagoner, R. Weinmeister, and D. Jensen. 2008. Comparison of low-moisture blocks and salt for manipulating grazing patterns of beef cows. Journal of Animal Science 86:1271–1277.

Barnowe-Meyer, K. K., P. J. White, T. L. Davis, D. W. Smith, R. L. Crabtree, and J. A. Byers. 2010. Influences of wolves and high elevation dispersion on reproductive success of pronghorn (*Antiliocapra americana*). Journal of Mammalogy 91:712–721.

Baudains, T. P., and P. Lloyd. 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Animal Conservation 10:400–407.

Beale, D. M., and A. D. Smith. 1970. Forage use, water consumption, and productivity of pronghorn antelope in western Utah. Journal of Wildlife Management 34:570–582.

Berger, J., D. Daneke, J. Johnson, and S. H. Berwick. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biological Conservation 25:193–208.

Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: Use and misuse of habituation, sensitization and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395:177–185.

Boccadori, S. J., P. J. White, R. A. Garrott, J. J. Borkowski, and T. L. Davis. 2008. Yellowstone pronghorn alter resource selection after sagebrush decline. Journal of Mammalogy 89:1031–1040.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421–431.

Bright, J. L., and C. Van Riper. 2001. The influence of habitat types, water sources, and movement barriers on pronghorn antelope home ranges in Northern Arizona. Pages 33–40 *in* C. Van Riper, K. A. Thomas, and M. A. Stuart, editors. Proceedings of the Fifth Biennial Conference of Research on the Colorado Plateau, Flagstaff, Arizona, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multi-model inference. Springer-Verlag, New York, New York, USA.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press, Chicago, Illinois, USA.

Canon, S. K. and F. C. Bryant. 1997. Bedsite characteristics of pronghorn fawns. Journal of Wildlife Management 61:1134–1141.

Clary, W. P., and D. M. Beale. 1983. Pronghorn reactions to winter sheep grazing, plant communities, and topography in the Great Basin. Journal of Range Management 36:749–752.

Clemente, F., R. Valdez, J. L. Holechek, P. J. Zwank, and M. Cardenas. 1995. Pronghorn home range relative to permanent water in southern New Mexico. The Southwestern Naturalist 40:38–41.

Cogan, D., H. Marriott, M. Pucherelli. 2004. Custer State Park, South Dakota, vegetation mapping project. Technical Memorandum 8260-04-01, U. S. Bureau of Reclamation Technical Service Center, Remote Sensing and GIS Group, Denver, Colorado.

CSP. 1995. Custer State Park resource management plan 1995–2010. Unpublished document.

D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736–744.

Dow, S. A., and P. L. Wright. 1962. Changes in mandibular dentition associated with age in pronghorn antelope. Journal of Wildlife Management 26:1–18.

Duong, T. 2009. ks: Kernel smoothing. R package version 1.6.8. http://CRAN.R-project.org/package=ks

Dzialak, M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, and L. D. Hayden-Wing. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. PLoS ONE 6: [online] e14597. doi10.1371/journal.pone.0014597

Ecological Software Solutions, 2007. LOAS Version 4.0. [software] Ecological Software Solutions, Sacramento, California, USA.

Environmental Systems Research Institute. 2006. ArcGIS: Release 9.2 [software] Redlands, California: Environmental Systems Research Institute, 1999–2006.

Fairbanks, W. S., and R. Tullous. 2002. Distribution of pronghorn (Antilocapra Americana) on Antelope Island State Park, Utah, USA, before and after establishment of recreational trails. Natural Areas Journal 22:277–282.

Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildlife Society Bulletin 14:63–68.

Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? Canadian Journal of Zoology 84:1775–1780.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gillingham, M. P., and K. L. Parker. 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. Alces 74:7–20.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed kernel analysis of animal range use. Journal of Wildlife Management 70:1334–1344.

Guenzel, R. J. 1986. Pronghorn ecology in southcentral Wyoming. Thesis, University of Wyoming, Laramie, Wyoming, USA.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Interpreting resource selection at different scales for woodland caribou in winter. Journal of Wildlife Management 70:1601–1614.

Haskill, S. P., and W. B. Ballard. 2008. Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. Canadian Journal of Zoology 86:627–637.

Hervert, J. J., J. L. Bright, R. S. Henry, L. A. Piest, and M. T. Brown. 2005. Home-range and habitat-use patterns of Sonoran pronghorn in Arizona. The Wildlife Society Bulletin 33:8–15.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Devlopment of a 2001 national land cover database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Hughes, K. S., and N. S. Smith. 1990. Sonoran pronghorn use of habitat in southwest Arizona. Research Report 146-0091564, Arizona Cooperative Fish and Wildlife Research Unit, University of Arizona, Tucson, Arizona, USA.

Jenness, J. 2010. DEM Surface Tools (surface_area.exe) v.2.0.230. [software] Jenness Enterprises. Available at: http://www.jennessent.com/arcgis/surface_area.htm.

Jones, R. L., and H. C. Hanson. 1984. Mineral licks, geophagy, and biogeochemistry of North American ungulates. Iowa State Press, Ames, Iowa, USA.

Kolar, J. L. 2009. Pronghorn migration and resource selection in southwestern North Dakota. Thesis, University of Missouri, Columbia, Missouri, USA.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760–770.

MacArthur, R. A., V. Geist, and R. H. Johnston. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. The Journal of Wildlife Management 46:351–358.

MacKenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. The Journal of Wildlife Management 70:367–374.

Manly, B. F., L. L. MacDonald, D. L. Thomas, T. L. MacDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411–1427.

McLoughlin, P. D., D. W. Morris, D. W., Fortin, D., Vander Wal, E., and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4–12.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing. Journal of Wildlife Management 64:994–1003.

Morgart, J. R., J. J. Hervert, P. R. Krausman, J. L. Bright, and R. S. Henry. 2005. Sonoran pronghorn use of anthropogenic and natural water sources. Wildlife Society Bulletin 33:51–60.

Nudds, T. D., and M. L. Morrison. 1991. Ten years after "reliable knowledge": Are we gaining? Journal of Wildlife Management 55:757–760.

R Development Core Team. 2009. R: A language and environment for statistical computing. [software] R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293–313.

Rouse, C. H. 1959. Antelope-range relationships. Interstate Antelope Conference Transactions 2:4–9.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. 63:739–747.

Schwartz, C. C., J. G. Nagy, and R. W. Rice. 1977. Pronghorn dietary quality relative to forage availability and other ruminants in Colorado. Journal of Wildlife Management 41:161–168.

SDGFP. 2005. South Dakota Mountain Lion Management Plan: 2003–2005. 3rd Working Draft Version 05-2. South Dakota Department of Game, Fish and Parks. Pierre, South Dakota, USA.

Selting, J. P., and L. R. Irby. 1997. Agricultural land use patterns of native ungulates in southeastern Montana. Journal of Range Management 50:338–345.

Stewart, K. M., R. T. Bowyer, J. G. Kie, and M. A. Hurley. 2010. Spatial distributions of mule deer and North American elk: resource partitioning in a sage-steppe environment. The American Midland Naturalist 163:400–412.

Thomas, D. L., and E. .J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322–330.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

Wydeven, A. P. and Dahlgren, R. B. 1985. Ungulate habitat relationships in Wind Cave National Park. Journal of Wildlife Management 49:805–813.

Yoakum, J. D. 2004. Foraging ecology, diet studies and nutrient values. Pages 447–502 *in* B. W. O’Gara, and J. D. Yoakum, editors. Pronghorn ecology and management. University Press of Colorado, Boulder, Colorado, USA.

Table 1. Hypotheses and corresponding *a priori* models explaining seasonal pronghorn resource selection in Custer State Park, South Dakota, October 2005 - August 2008.

Hypothesis	Model
Forage	$\beta_0 + \beta 1$(cool-season grass biomass) + $\beta 2$(warm-season grass biomass) + $\beta 3$(forb biomass) + $\beta 4$(shrub patch density^a)
Water	$\beta_0 + \beta_1$(distance to stream^a) + β_2(distance to pond^a)
Thermoregulation	$\beta_0 + \beta_1$(solar radiation) - β_2(canopy cover^a)
Predator avoidance	$\beta_0 - \beta_1$(terrain ruggedness) + β_2(distance to forest^a)
Total disturbance	$\beta_0 - \beta_1$(total disturbance density^a) - β_2(visibility)
Predictable disturbance	$\beta_0 - \beta_1$(predictable disturbance density^a) - β_2(visibility)
Unpredictable disturbance	$\beta_0 - \beta_1$(unpredictable disturbance density^a) - β_2(visibility)
Forage- water interaction	$\beta_0 - \beta_1$forb biomass) - β_2(shrub patch density^a) + β_3(inverse distance to water) + β_4(forb biomass × inverse distance to water) + β_5(shrub patch density^a ×inverse distance to water)

[a] = Pseudo-threshold transformation of variable

Table 1, continued.

Hypothesis	Model
Forage - flatness interaction	$\beta_0 - \beta_1$(forb biomass) - β_2(shrub patch density[a]) + β_3(inverse terrain ruggedness) + β_4(forb biomass × inverse terrain ruggedness) + β_5(shrub patch density[a] ×inverse terrain ruggedness)
Forage-disturbance interaction	$\beta_0 - \beta_1$(forb biomass) - β_2(shrub patch density[a]) + β_3(inverse distance to disturbance) + β_4(forb biomass × inverse distance to disturbance) + β_5(shrub patch density[a] ×inverse distance to disturbance)
Forage and mineral sites	$\beta_0 + \beta_1$(forb biomass) + β_2(shrub patch density[a]) - β_4(distance to mineral site)
Habitat type	$\beta_0 - \beta_1$(barren) - β_2(coniferous forest) - β_3(deciduous forest) - β_4(floodplain woodland) - β_5(urban) + β_6(prairie dog) - β_7(post-fire) - β_8(riparian shrubland) + β_9(grassland) + β_{10}(shrubland) - β_{11}(wetland)

Table 2. Number of times (*n*) each hypothesis received the most support based on Akaike weights (w_i) and mean and range of Akaike weights for individual pronghorn resource selection in Custer State Park, South Dakota, for fall, winter, spring, and summer, 2005–2008.

	Fall w_i			Winter w_i			Spring w_i			Summer w_i		
Model	*n*	$\bar{x}$	Range	*n*	$\bar{x}$	Range	*n*	$\bar{x}$	Range	*n*	$\bar{x}$	Range
Forage							3	1.00	0.99–1.00	2	0.86	0.76–0.95
Water	7	1.00	0.98–1.00	7	0.97	0.80–1.00	6	0.95	0.68–1.00	3	0.92	0.84–1.00
Predictable Disturbance	1	1.00					4	1.00		4	0.88	0.60–1.00
Unpredictable Disturbance	2	1.00		1	0.76		3	1.00		3	1.00	0.99–1.00
Total Disturbance										1	1.00	

Table 2, continued.

	Fall w_i			Winter w_i			Spring w_i			Summer w_i		
Model	*n*	$\bar{x}$	Range	*n*	$\bar{x}$	Range	*n*	$\bar{x}$	Range	*n*	$\bar{x}$	Range
Forage and Mineral Sites	10	1.00	0.98–1.00	9	0.98	0.85–1.00	19	1.00	0.99–1.00	16	0.95	0.55–1.00
Forage and Water	10	0.98	0.80–1.00	12	1.00	0.98–1.00	10	1.00		15	0.97	0.55–1.00
Forage and Total Disturbance	8	1.00	0.99–1.00	11	0.99	0.88–1.00	21	0.98	0.62–1.00	11	0.97	0.75–1.00
Predator Avoidance							1	1.00				
Habitat Type							1	0.96				

Table 3. Parameter estimates (β) and standard errors (SE) from population-level resource utilization functions for pronghorn at Custer State Park, South Dakota, for fall, winter, spring and summer, 2005–2008.

	Fall		Winter		Spring		Summer	
Parameter	β	SE	β	SE	β	SE	β	SE
Intercept	452.98	55.77	3673.63	353.89	5980.33	815.05	975.31	147.65
Distance to stream[a] (m)	18.78	8.91	52.33	40.05	-85.48	89.56	13.30	10.20
Distance to pond[a] (m)	-37.70	19.32	-64.32	28.90	15.15	115.87	-15.10	24.60
Predictable disturbance density[a] (km/km^2)	13.16	13.20			27.29	27.95	-4.39	9.67
Unpredictable disturbance density[a] (km/km^2)	-16.08	12.26	-21.94	21.94	-96.25	62.43	-55.60	40.83
Total disturbance density[a] (km/km^2)							3.40	3.40

[a] = Pseudo-threshold transformation of variable, [b] = density of shrub patches per km^2

Table 3, Continued.

	Fall		Winter		Spring		Summer	
Parameter	β	SE	β	SE	β	SE	β	SE
Distance to visible road (m)	1.34	1.16	-3.31	3.31	-11.13	11.61	-8.98	5.07
Cool season grass biomass (kg)	-0.54	3.07			-2.82	1.87	1.24	3.03
Warm season grass biomass (kg)	-0.02	3.53			9.51	5.91	3.80	3.08
Forb biomass (kg)	-8.55	15.44	545.69	147.14	357.03	563.18	-51.50	96.69
Shrub patch density[b]	-84.12	121.62	1577.97	495.99	972.54	1108.35	194.23	144.07
Distance to mineral sites[a] (m)	-27.24	22.47	-140.50	54.47	-315.74	223.89	5.55	33.90
Inverse distance to water	21.16	18.82	267.20	108.91	22.16	58.53	18.90	37.98

[a] = Pseudo-threshold transformation of variable, [b] = density of shrub patches per km^2

Table 3, continued.

	Fall		Winter		Spring		Summer	
Parameter	β	SE	β	SE	β	SE	β	SE
Forb biomass × inverse distance to water	-5.89	19.58	-166.68	100.72	123.21	219.23	-42.51	23.27
Shrub patch density × inverse distance to water	46.31	72.43	-209.46	342.61	488.94	312.17	-51.73	78.76
Inverse total disturbance density	-54.48	40.15	-8.04	31.51	-334.60	534.39	-61.75	65.44
Forb biomass × inverse disturbance density	20.11	18.46	-348.98	130.82	-238.89	543.08	176.72	145.56
Shrub patch density × inverse disturbance density	67.75	90.11	-1035.65	347.26	-784.02	1118.01	-59.62	121.03

[a] = Pseudo-threshold transformation of variable, [b] = density of shrub patches per km^2

Table 3, continued.

	Fall		Winter		Spring		Summer	
Parameter	β	SE	β	SE	β	SE	β	SE
Surface ratio					1.94	2.23		
Distance to forest[a] (m)					136.44	121.43		
Coniferous forest[c]					-0.57	0.57		
Deciduous forest[c]					-0.03	0.03		
Floodplain woodland[c]					-0.27	0.27		
Urban[c]					0.01	0.01		
Prairie dog colony[c]					0.66	0.66		
Post-fire vegetation[c]					-0.03	0.03		
post-fire vegetation[a]					-0.06	0.06		
Upland grassland[c]					-0.30	-0.30		

[a] = Pseudo-threshold transformation of variable, [c] = levels of the categorical habitat model

Table 3. Continued.

	Fall		Winter		Spring		Summer	
Parameter	β	SE	β	SE	β	SE	β	SE
Upland shrubland[c]					-0.03	0.03		
Wetland herbaceous vegetation[c]					-0.03	0.03		

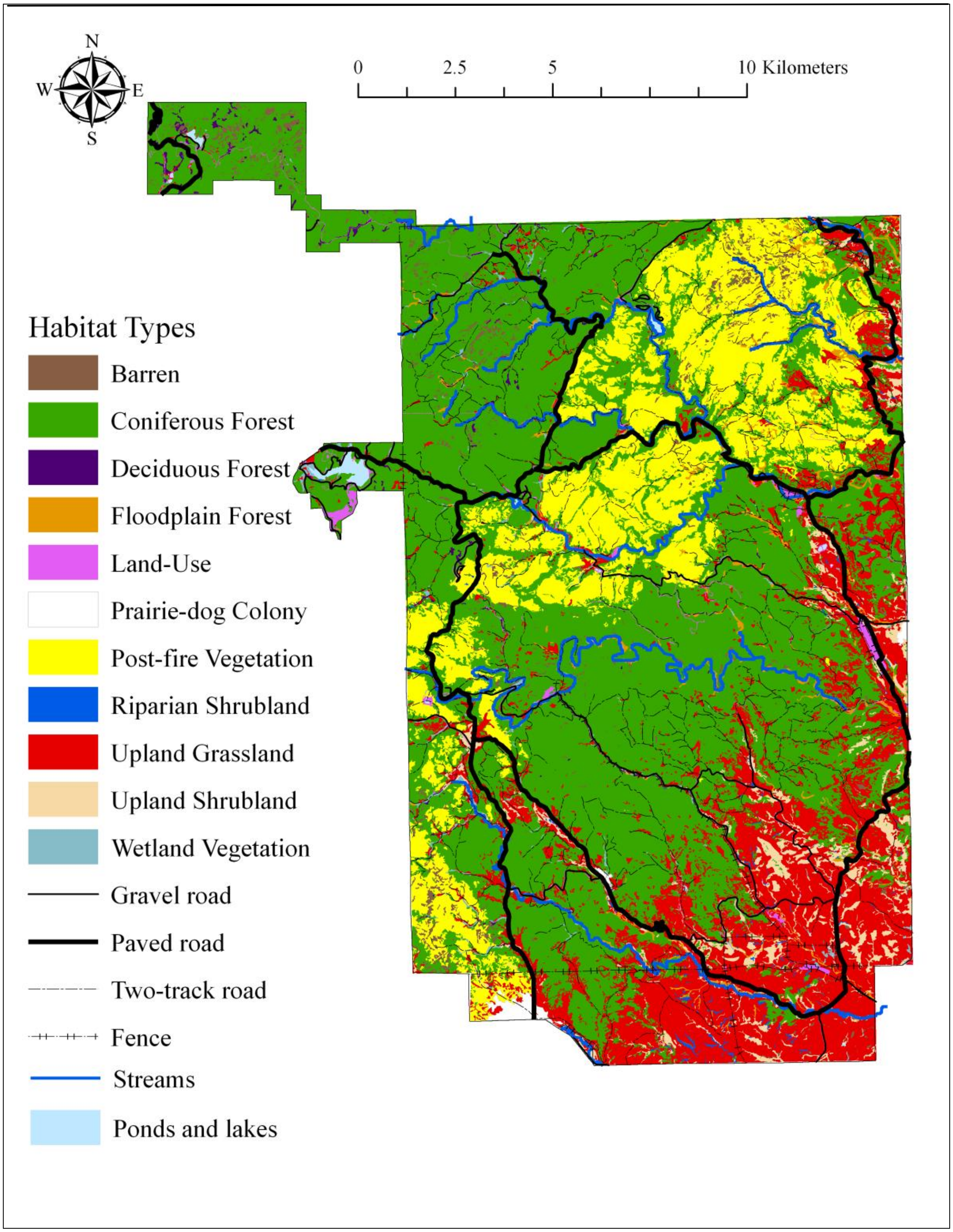

Figure 1. Major habitat types and features of Custer State Park, SD.

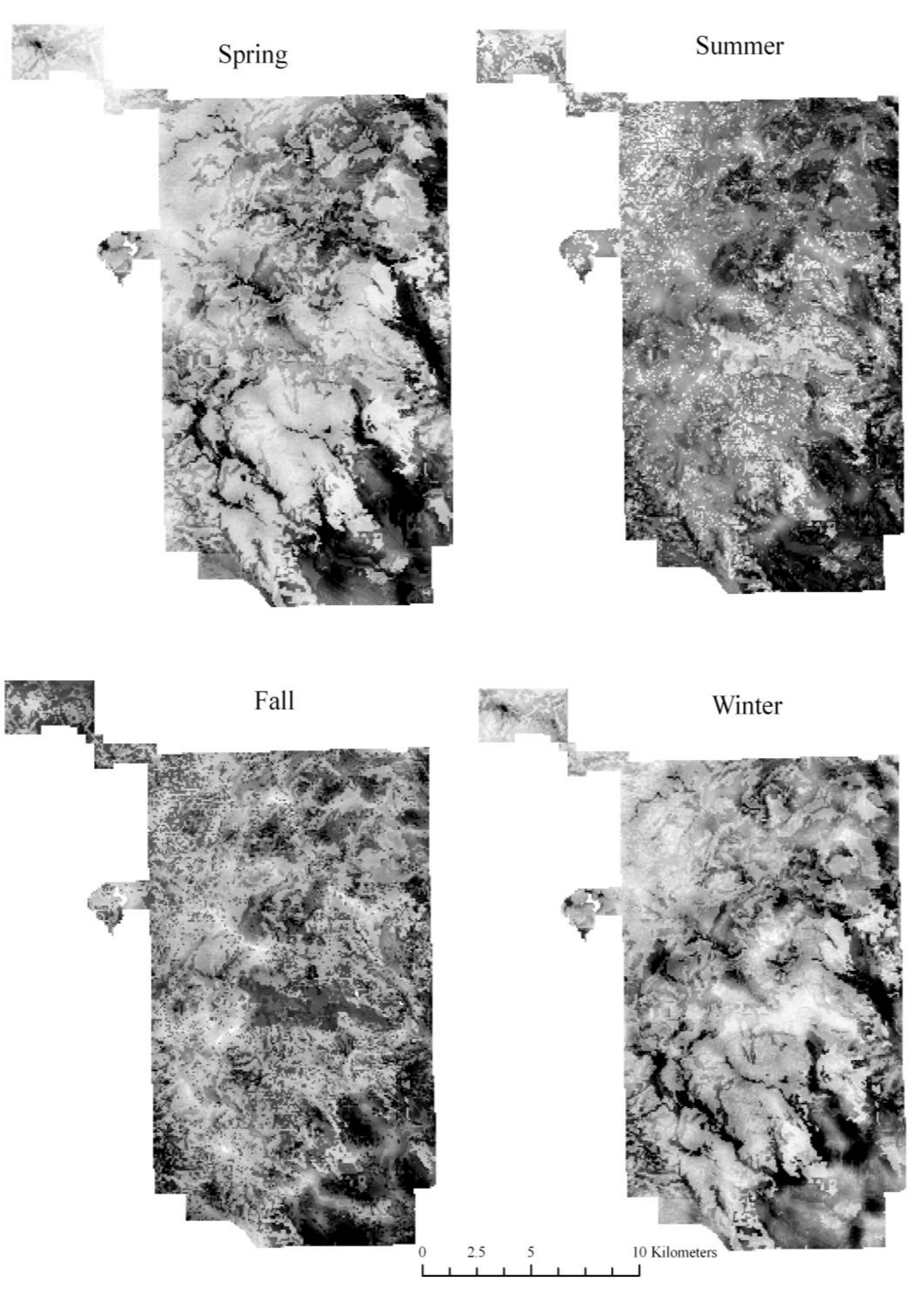

Figure 2. Spatial patterns of predicted selection for pronghorn during spring, summer, fall and winter in Custer State Park, SD, 2005-2008. Relative probability of occurrence ranges from low (light) to high (dark).

CHAPTER IV. DIET COMPOSITION AND OVERLAP OF AN UNGULATE ASSEMBLAGE IN THE BLACK HILLS, SOUTH DAKOTA

ABSTRACT

Resource competition, particularly diet overlap, is the main factor dictating the diversity and size of coexisting ungulate populations. We studied diet composition and overlap in an ungulate assemblage in Custer State Park (CSP), South Dakota, to estimate carrying capacity. We used microhistological techniques to estimate diet composition of each ungulate species, and calculated Schoener's index of dietary overlap, which ranges from 0 (complete separation) to 1 (complete overlap), between each species pair. Diet composition of each species followed *a priori* expectations based on the physiology and natural history of the species. Bison (*Bison bison*) were bulk grazers; annual diets consisted primarily of cool-season grasses (57.9%), warm-season grasses (21.7%), and sedges (15.4%), and only small amounts (4.9%) of shrubs and forbs. The composition of warm-season grasses in bison diets was highest during the summer (31.9%) and lowest during the winter (15.9%). Elk (*Cervus elaphus*) fed intermediately on grass and forbs and shrubs; annual diets consisted of primarily grass (63.1%), and moderate amounts of shrubs (25.7%) and forbs (10.2%). However, during spring grass composition was > 80% of elk diets, elk may be considered bulk grazers during this time period. Pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) were concentrate selectors. Annual pronghorn diets were

primarily split between forbs (48.2%) and shrubs (40.4%), and grasses made up 9.8% of their diet. Graminoids accounted for a greater proportion of pronghorn diets during spring (16.8%) and summer (12.0%) compared to fall (7.6%) and winter (3.0%). Mule deer diets were predominately shrubs (72.7%) although forbs were important as well (22.9%); grasses made up only 5.1% of mule deer diets. Dominant forage species in mule deer diets included leadplant (*Amorpha canescens*), ponderosa pine (*Pinus ponderosa*), western snowberry (*Symphoricarpus albus*), fringed sagewort (*Artemisia frigida*), and cudweed sagewort (*Artemisia ludoviciana*). We found consumption of ponderosa pine and fringed sagewort by mule deer to be 8.3–10.7 and 1.4–2.4 times higher, respectively, during the spring and winter. However, consumption of wild rose and western snowberry by mule deer were 1.4–27.5 and 4.8–12.9 times lower during spring and winter. White-tailed deer consumed more grass than the other concentrate selectors, with an annual diet composition that was 28.7% grass; however shrubs dominated their diets (55.1%) and forbs were an important component (16.2%). Ponderosa pine, wild rose (*Rosa* spp.), raspberry (*Rubus idaeus*), and snowberry were dominant shrub species and Kentucky bluegrass (*Poa pratensis*) and western wheatgrass (*Pascopyrum smithii*) were dominant grass species in white-tailed deer diets. The proportion of western wheatgrass in white-tailed deer diets was 1.7–4.6 times higher during the spring compared to other seasons, and composition of ponderosa pine in diets during spring and winter was 3.8–18.9 times higher than during fall and summer. Overall, annual dietary overlap was high between bison and elk (0.63), elk and white-tailed deer (0.60), pronghorn and mule deer (0.61), and moderate between white-tailed deer and mule deer (0.55). Annual overlap was lowest between bison and mule deer

(0.08) and bison and pronghorn (0.16). In general, dietary overlap among ungulate species was greatest during the summer and lowest during the winter. Overlap was high to moderate (> 0.50) between bison and elk, and elk and white-tailed deer during every season, and for pronghorn and mule deer during the summer and winter, white-tailed deer and pronghorn during the summer and fall, white-tailed deer and mule deer during the fall, and elk and pronghorn during the summer. If managers aim to reduce or eliminate competition between bison and elk, and white-tailed deer and elk, we recommend management actions that would increase the biomass of palatable warm- and cool-season grasses, and shrub species such as leadplant and wild rose. Our results provide evidence that in areas that support large diverse ungulate assemblages, especially those that are closed to dispersal, substantial dietary overlap may exist even when each species forages within their evolutionary niches.

INTRODUCTION

The ability of ungulate species to coexist depends largely on the partitioning of resources, particularly diet. Typically, ungulate species that are similar in one dimension (e.g., diet) differ in other dimensions (e.g., space-use) to promote coexistence, while reducing competition (Leuthold 1978, Bodmer 1991, Prins and Fritz 2008). However, complete separation of both space-use and diet composition is rare in a natural setting, especially as the number of ungulate species increases (Putnam 1996, Bagchi et al. 2003, Prins and Fritz 2008). In general, diet selection in ungulates is based on the quality and quantity of forage and is often a trade-off between the most nutritious forage and its availability compared to other abundant, less nutritive forage species (Putnam 1988). Diet selection is guided by a series of morphological features, namely; body size, rumeno:reticular volume to body weight ratio, and mouth size (Hanley 1982, Illius and Gordon 1987, Putnam 1988). Knowledge of diet selection is essential in evaluating potential competitive interactions and determining rangeland carrying capacity.

The Northern Great Plains eco-region is an area of historically high ungulate species diversity in North America. Large roaming herds of bison (*Bison bison*) were interspersed with pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis* Audubon) over great expanses of open prairie. Custer State Park (CSP), in the Black Hills of South Dakota, is one site where a high diversity of ungulates still exist, many of them (bison, elk and pronghorn) at a relatively high density that provides excellent wildlife viewing opportunities for the public. The ecotone of mixed-grass prairie and ponderosa pine woodland on the Black Hills foothills is also an area of high vegetative biodiversity, as it consists of species native to both the Great Plains and the Rocky Mountains (Larson and Johnson 1999). The park actively manages ungulate populations through annual culling operations to maintain the health and productivity of both the ungulate assemblage and the rangeland. Decisions on the population sizes of ungulate species that can co-occur are based on assumptions of the resource use of each species, including diet selection and overlap.

Ungulate diets can be highly variable and site-specific (Yoakum 2004, Cook 2002, Christianson and Creel 2007). Factors such as human disturbance (Skogland and Grovan 1988, Edge et al. 1987, Jiang et al. 2007), predation (Berger 1978, Ripple and Beschta 2006), security cover (Roloff et al. 2001, Skolvin et al. 2002), and intraspecific competition (Belovesky 1997, Gordon and Illius 1989, Murray and Illius 2000) can influence foraging decisions by ungulates. Based on the morphological characteristics of each ungulate (Hanley 1982, Hofmann 1985), bison should be primarily bulk-feeding grazers of low-quality forage, elk should be intermediate adaptive-selective grazers, mule deer and pronghorn should be selective concentrate selectors, and white-tailed deer should be opportunistic adaptable concentrate selectors. However, CSP is an area of high human-related disturbance (including hunting), ungulate density, and supports an active predator community (mountain lions [*Puma concolor*], coyotes [*Canis latrans*], bobcats [*Lynx rufus*], and golden eagles [*Aquila chrysaetos*]). Further, it is primarily a closed system, which may affect the ability of each ungulate to forage within these classifications.

Based on the foraging strategies reported in the literature for the ungulate assemblage in CSP, we would expect overlap in diet between ungulates that are close to each other on the grazer-browser spectrum. Thus, we predict those at the opposite edges of the spectrum, such as bison and mule deer, would exhibit very little overlap while those close to each other, such as bison and elk, would exhibit a greater degree of overlap. There is evidence that elk overlap in diet with bison, white-tailed deer and mule deer where these species coexist (Cook 2002). Wydeven and Dahlgren (1985) found potential competition between elk and pronghorn, elk and mule deer, and elk and bison in Wind Cave National Park, directly adjacent to CSP. Other studies have reported high dietary overlap between pronghorn and mule deer as well (McCullough 1980, Bailey and Cooperrider 1982, Singer and Norland 1994, Hansen et al. 2001).

To improve knowledge of ungulate resource use in CSP, our goals were to 1) determine diet composition of each ungulate species in CSP, and 2) determine diet overlap among ungulates in CSP.

STUDY AREA

Custer State Park is composed of 286.32 km^2 of rangeland and forest common to the southern Black Hills region in southwestern South Dakota. Steep granite spires characterize the northwest portion of the Park, undulating forested hills interspersed with areas of fire-killed forest dominate the central portion, and grasslands dominate the eastern and southern portions of the Park (CSP 1995; Figure 1). Elevations range from 1,146–2,042 meters (CSP 1995).

The mixed-grass prairie and upland shrubland ecosystem compose approximately 21% (6,105 ha) of CSP (CSP 1995; Figure 1). Grasslands are dominated by Kentucky bluegrass (*Poa pratensis*), big bluestem (*Andropogen gerardi*), little bluestem (*Andropogen scoparius*), western wheatgrass (*Agropyron smithi*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*) and sedges (*Carex* spp.; CSP 1995). Dominant shrub species include leadplant (*Amorpha canscens*), western snowberry (*Symphoricarpus albus*), wild raspberry (*Rubus ideaus*), and wild rose (*Rosa* spp.).

Over half (55%) of CSP is covered by forest. The central forested portion of CSP is dominated by ponderosa pine (*Pinus ponderosa*) which shifts to a mixture of ponderosa pine and white spruce (*Picea glauca*) on northern slopes and high elevations (Figure 1). A small amount of deciduous forest (2% of CSP) is characterized by predominantly bur oak (*Quercus macrocarpa*) and trembling aspen (*Populus tremmuloides*) forest occurs primarily in riparian corridors (Figure 1). Stand structure diversity in CSP consists of 52.33 km^2 of single-story forest and 71.49 km^2 of multi-story forest (CSP 1995). Woodland understory communities in CSP are dominated by Kentucky bluegrass (*Poa pratensis*), poverty oatgrass (*Danthonia spicata*), sedges (*Carex* spp.), bearberry (*Arctostaphylos uva-ursi*), wild raspberry (*Rubus ideaus*), and western snowberry (*Symphoicarpus occidentalis*; Custer State Park, unpublished data). Almost 30% of CSP is burned-over forest, results of the Galena fire of 1988, the Cicero Peak fire of 1990, and the Four-mile fire of 2008. Fire-damaged forest consists of 109.79 km^2, 60% of which is fire-killed where nominal regeneration has occurred and where the canopy remains open (CSP 1995; Figure 1).

A 1.54 m woven-wire fence surrounds the majority of CSP except for a small portion in the northwestern corner of the Park. This fence prevents movement of bison but allows for movement of all other ungulate species into or out of CSP, although there is evidence that pronghorn and elk do not frequently cross the fence (B. Keller, and J. Millspaugh, unpublished data). There are three other internally fenced areas in CSP, which create three distinct pastures in CSP and are used to move bison during the roundup and to manage grazing of bison throughout the year (Figure 1).

For 1992–2008, annual precipitation for CSP averaged 49.86 cm and ranged from 74% to 161% of the 25-year mean. Approximately 76% of precipitation in CSP fell from April to September (unpublished data). Winter in the southern Black Hills is considerably more mild than elsewhere in the region, and a persistent snowpack was not typically present during the study period. Average snowfall for the southern Black Hills is 32.0 cm; March is the snowiest month with an average snowfall of 18.8 cm. Temperatures in CSP are more moderate than the surrounding plains; the average annual,

summer and winter temperature in CSP is 6.7° C, 16° C, and –5° C, respectively (CSP 1995).

Approximately 800–1000 bison, 408–718 elk, 163–279 pronghorn, 867 white-tailed deer, 285 mule deer, 38 bighorn sheep, and 35–40 feral burros (*Equus asinus*) occupied CSP during our study period (C. Lehman, Custer State Park, personal communication). Bison were culled annually during the fall bison roundup, as well as during several hunts during the fall. Elk, white-tailed deer, and mule deer were also culled during fall hunting seasons. Coyotes (*Canis latrans*), mountain lions (*Felis concolor*) and bobcats (*Felis rufus*) were the major predators in CSP.

METHODS

We used microhistological analysis of fecal material to determine diet composition of each ungulate species in CSP. Microhistological analysis of feces is a widely used method to determine diet composition of ungulates (Holechek et al. 1982). Although some plants may be under- or over-estimated in ruminant diets due to differing digestabilities (Vavra and Holechek 1980, Dearden et al. 1975), this technique generally performs well to determine ungulate diet composition (Alipayo et al. 1992).

Sample collection

We collected fecal samples from each ungulate species in CSP on a weekly basis May 2005–January 2008. We attempted to collect at least 5 samples per ungulate species per week, 2005–2008, but this sampling frequency was only met for bison and pronghorn, and other ungulate species were sampled on a more opportunistic basis. This process resulted in an unequal sample size for each ungulate species (Table 1). We sought an equal collection of samples from throughout the park area, and purposefully visited different habitats (burned, forested, and prairie habitats) in different geographical regions of CSP (northeast, middle, southwest) to collect samples. We stratified fecal collection by habitat type and geographical region to ensure samples were an adequate representation of ungulate diets; not because we intend to draw any significance in diets among different regions or habitat types.

Because mule deer and white-tailed deer were sympatric in the Black Hills, and pellets are difficult to distinguish between deer species, we observed defecation prior to sample collection. We collected fresh (wet and dark) samples from the other species (elk, bison, and pronghorn) based on field identification. We air-dried samples in cheese cloth for approximately 48 hours or until completely dry; dried samples were stored in cheese cloth until they were ground for analysis.

Slide preparation

We ground each sample using a Wiley mill (Swedesboro, NJ) with a 1-mm screen. We used microhistological fecal analysis to determine percent occurrence of forage species within each sample. We composited samples for each ungulate species by week. Individual variability is generally low among ungulate diets in this region (Zimmerman 2004), and compositing of individual samples is common practice in diet studies (Alipayo et al. 1992, Gibbs et al. 2004, Beck and Peek 2005). Jenks et al. (1989) found no difference in diet quality (fecal nitrogen) estimates based on composited and individual samples.

Approximately 1 teaspoon of ground fecal matter was used from each sample to determine diet. Composited samples were soaked in household bleach (6% sodium hypochlorite) until cleared (Holechek and Valdez 1985), and then washed in a 0.0074 mm sieve until the sample no longer reacted with water (bubbled) or smelled of bleach. We used a Phenol-glycerol solution (Davitt and Nelson 1980) to mount samples to slides for ease in identification.

Reference slides

We prepared reference slides of plant material collected from CSP. We prepared slides of 11 shrub species, 22 grass and sedge species, and 46 forb species using the same methods as above. We used a 100–400× trinocular microscope to digitally photograph reference slides.

Slide interpretation

We used a random number generator to identify coordinates on the microscope grid for 15 fields of view from each slide. We identified the plant fragment nearest to the field of view. We used cell wall structure, shape and size of cells, trichomes and hair presence and structure, and stomata size and structure to identify plant fragments by comparing them to reference slides. We only identified fragments a minimum of 5 micrometers in size and with 2-3 identifiable characteristics.

Data analysis

We determined the percent coverage of each forage species by summing the area occupied by each species and dividing by the total area occupied within slides (15). We calculated mean and standard errors of percent coverage of each forage species for each ungulate species for each season (fall = 1 September – 30 November, winter = 1 December – 29 February, spring = 1 March – 30 May, summer = 1 June – 31 August).

We first averaged each year separately, and then averaged across years so that each year of data collection was equally represented in the overall average.

We used Schoener's index (1968) to calculate seasonal and overall diet overlap among ungulate species. Schoener's index is calculated as:

$$O_{jk} = 1 - \frac{1}{2}\left(\sum \left|P_{ij} - P_{ik}\right|\right)$$

where O_{jk} is the overlap index between species *j* and species *k*, P_{ij} is the proportion of plant species *i* in the diet of ungulate species *j*, and P_{ik} is the proportion of plant species *i* in the diet of ungulate species *k*. Schoener's index ranges from 0, where there is no overlap in diets between two ungulate species, and 1, where diet overlap is complete between two ungulate species (Gordon and Illius 1989), a Schoener's index of ≥ 0.60 is generally considered biologically significant (Schoener 1968).

RESULTS

Bison

Grasses dominated bison diets during all seasons (Figure 2), and blue grama (*Bouteloua gracilis*), Kentucky bluegrass, sedges (*Carex* spp.) and western wheatgrass were the dominant grass species consumed by bison (Table 2). Shrub and forb species were minor components of bison diets (Table 2). Based on the large amount of grass in bison diets, CSP bison fell within the 'bulk grazer' classification of Hanley (1982). Bison consumed more grass and less forb and shrubs compared to other ungulates (Figure 3). Plant species diversity was highest in bison diets during the summer (23 forage species), followed by the winter (20 species) and the spring and fall (18 species). Although cool-season grasses dominated bison diets during every season, the composition of warm-season grasses in bison diets was highest during the summer and lowest during the winter.

Elk

Elk were intermediate grazers in CSP; grasses dominated elk diets, but shrub and forb species made up moderate amounts of seasonal elk diets (Figures 2 and 3). However, during spring grass composition was > 80% of elk diets, and thus elk may be considered bulk grazers during spring (Figure 2). We identified 11 species of grass, 10 species of shrubs, and 15 species of forbs in elk diets (Table 3). Kentucky bluegrass, sedges, and western wheatgrass were the dominant grass species in elk diets (Table 3). Shrub and forb species were both moderate to minor components of elk diets, depending on the season (Figure 2). Consumption of forbs by elk was lowest during the winter and highest during the summer (Figure 2). Common yarrow (*Achillea millefolium*) and cudweed sagewort were the dominant forb species in elk diets.

Pronghorn

Pronghorn diets were dominated by forbs and shrubs during all seasons (Figures 2 and 3, Table 4), they were thus classified as concentrate selectors. Leadplant, wild raspberry, wild rose, and snowberry were dominant shrubs, and fringed sagewort and cudweed sagewort were the most frequent forb species in pronghorn diets (Table 4). Although grass was a minor component of pronghorn diets during all seasons (Figure 2), grass composition was greatest during the spring and summer and lowest during the fall and winter. Plant species diversity in pronghorn diets was similar during spring, summer and fall (20–22 species) and lowest during the winter (12 species). We identified 9 grass species, 6 shrub species, and 8 forb species in pronghorn diets (Table 4).

Mule deer

Mule deer were also concentrate selectors in CSP; shrub and forb species dominated diets, while grasses were a minor component (Figures 2 and 3). Mule deer consumed less grass and more forb and shrubs than other ungulate species in CSP (Figure 3). Leadplant, ponderosa pine, wild rose, and snowberry were the dominant shrub species, and cudweed sagewort and fringed sagewort were the dominant forb species in mule deer diets (Table 5). Fall was the period of highest forage diversity in mule deer diets (24 plant species), followed by winter (14), spring (12), and summer (11 species). We identified 8 grass species, 9 shrub species, and 8 forb species in mule deer diets (Table 5).

White-tailed deer

White-tailed deer diets were dominated by shrubs, but grasses were also frequently consumed, and seasonal variation was high (Table 6, Figures 2 and 3). White-tailed deer were thus classified as concentrate selectors, although the species consumed almost 3 times more grass than pronghorn and 5 times as much grass as mule deer. Ponderosa pine, wild rose, raspberry, and snowberry were dominant shrub species and Kentucky bluegrass and western wheatgrass were dominant grass species in white-tailed deer diets. Clover (*Trifolium* spp), cudweed sagewort, and common yarrow were the most frequently consumed forb species in white-tailed deer diets (Table 6). Species diversity of white-tailed deer forage consumption was highest during summer (34 species), moderate during spring and fall (21–26 species), and lowest during winter (21 species). We identified 11 grass species, 11 shrub species, and 16 forb species in white-tailed deer diets (Table 6).

Diet overlap

As expected, we observed high dietary overlap between species pairs in CSP that were close to one another on the browser-grazer continuum; although the amount of overlap among species pairs was seasonally dynamic. Dietary overlap among the ungulate assemblage was greatest during the summer and fall and lowest during the winter and spring (Table 7). We observed high (≥0.6) dietary overlap between 4 pairs of species in CSP across all seasons. Two species pairs consistently demonstrated moderate (≥ 0.50) to high overlap during every season: elk and bison, and elk and white-tailed deer (Table 7). Bison and elk overlapped in consumption of grasses, and elk and white-tailed deer dietary overlap was attributed to similar consumption of Kentucky bluegrass, as well as leadplant and ponderosa pine. Pronghorn and mule deer exhibited moderate to high overlap in diet during summer and winter, and pronghorn and white-tailed deer overlapped moderately to high in diet during summer and fall (Table 7). Dietary overlap between mule deer and pronghorn was attributed to similar use of some forb and shrub species, particularly rose, raspberry, cudweed sagewort, and fringed sagewort. Pronghorn and white-tailed deer overlap was due to similar amounts of leadplant, raspberry, and rose consumption during the summer. White-tailed deer and mule deer overlapped moderately in diet during the fall only (Table 7), due to similar consumption of oak, raspberry, rose, and snowberry.

DISCUSSION

Diets were similar to what is expected based on the physiology and grazing strategies of each ungulate species. Bison consumed primarily grass, elk intermediately fed between grass and forbs or browse, while pronghorn and both deer species were primarily concentrate selectors. However, elk could be considered a grazer during the spring season, when elk select the highly-nutritious flush of new grass growth (Jones and Wilson 1987, Van Soest 1994), and white-tailed deer were slightly more intermediate with regards to grass consumption than the other two concentrate selectors, mule deer and pronghorn. Increases of grass in elk diets during spring have been noted elsewhere (Wydeven and Dahlgren 1983, Cook 2002), and in the vast literature regarding white-tailed deer food habits (Verme and Ullrey 1984), diet composition of 22–35% grasses, as we observed, is not uncommon, and lends support to Hofmann's (1985) distinction of the species as "adaptable opportunists". Wydeven and Dahlgren (1985) found similar diet partitioning in Wind Cave National Park (WICA), which borders CSP, where elk fed on a mixture of graminoids and forbs, mule deer fed extensively on browse, pronghorn fed on a mixture of grass and forbs, and bison fed on graminoids. However, elk diets in WICA contained 25% less grass, and mule deer and pronghorn diets contained 26% and 31% greater forb composition, respectively, during the winter than we observed in CSP. Similar separation of diets has also been reported for the ungulate assemblage in Yellowstone National Park (Singer and Norland 1994). However, diet separation in CSP was not complete, and the potential for competition does exist.

Diets for each species were similar to other studies in the general region (Bayless 1969, Messenger and Schitoskey 1980, Mitchell and Smoliak 1981, Hobbs et al. 1983, Wydeven and Dahlgren 1983, Wydeven and Dahlgren 1985, Zimmerman 2004), with a few exceptions that might be explained by differences in forage availability. Elk at the National Bison Range in Montana consumed diets of almost entirely grass during the majority of the year, and mule deer consumed diets of 84–97% grasses during spring

(Morris and Schwartz 1957). However, the authors noted the limited availability and palatability of the browse and forb content of the range during sampling. Sievers (2004) found that pronghorn consumed high amounts of grass in WICA, which contradicted both our findings and those of Wydeven and Dahlgren (1985) for the same study site. These differences may be due to lower availability of key forage species (cudweed sagewort and fringed sagewort) for pronghorn in WICA compared to CSP (Keller and Millspaugh 2010), differences that perhaps took place after the Wydeven and Dalhgren studies of the 1970's. White-tailed deer consumed more shrubs and less forb species than observed for other populations in the southern Black Hills (Zimmerman 2004). However grass consumption and composition was similar to reported in Zimmerman (2004). Mule deer diets in CSP were similar in overall composition to diets reported for mule deer in the southern Black Hills by Zimmerman (2004) and in WICA by Wydeven (1979).

Based on dietary overlap, potential for competition among ungulate species in CSP was greatest for bison and elk and white-tailed deer and elk, and increased from winter to summer. The amount of dietary overlap of elk and bison in CSP was similar to that reported for Yellowstone National Park (Singer and Norland 1994) and Wind Cave National Park (Wydeven 1979). However, Singer and Norland (1994) found no evidence that competition between bison and elk occurred in Yellowstone National Park during that time because there was no change in diet or habitat use of the two species in response to large fluctuations in population sizes. Given that elk have the ability to select from a much broader range of diets than bison, which are primarily restricted to bulk feeding, elk might have a competitive advantage over bison. However, factors such as human disturbance or predation tend to affect elk foraging patterns to a greater extent than bison

(Herdandez and Laundre 2005, Borkowski et al. 2006), especially in hunted populations such as CSP (Millspaugh et al. 2000, Profitt et al. 2010). Further, bison can utilize coarser forage than elk, and are more efficient at consuming large quanitites of relatively poor quality forage (Hanley 1982). Thus, with regards to the plant species which both ungulates consume, bison have the competitive advantage. The large population sizes of both of these ungulates in CSP will likely result in trade-offs between which population size can be maximized based on forage available and dietary overlap. The amount of available graminoids will likely be the limiting factor for coexistence of bison and elk in CSP. However, the decrease in dietary overlap as the growing season progresses may limit the potential for competition. High levels of dietary overlap during the beginning of the growing season, when nutritious forage is more abundant, is less likely to lead to competition than during times when resources are very limited, such as winter (Schoener 1982). However, even moderate levels of dietary overlap during winter, as observed for bison and elk, may lead to competition (Schoener 1982).

White-tailed deer may compete with both intermediate feeders and concentrate selectors given their diet consumption in CSP. Elk are sympatric with white-tailed deer in the northwestern United States and adjacent areas in Canada (Miller 2002) and several disjunct areas of the eastern United States where elk have been reintroduced. Rarely does the species overlap in the dry, ponderosa pine habitat typical of the Black Hills, so making direct comparisons between dietary overlap in other sympatric populations is tenuous. However, Jenkins and Wight (1988) found high dietary and moderate spatial overlap among white-tailed deer and elk during winter in northern Montana, and Kingery et al. (1996) found substantial dietary overlap between the two species in red cedar

(*Thuja plicata*) forests in northern Idaho. The high amount of dietary overlap we observed was primarily attributed to consumption of similar amounts of ponderosa pine during the winter, and leadplant and Kentucky bluegrass throughout the year. The two species are not likely to compete for consumption of ponderosa pine, due to its abundance in the Black Hills. Thus, Kentucky bluegrass and leadplant may be the limiting factors for populations of elk and white-tailed deer to coexist in CSP. White-tailed deer also overlap high to moderately with pronghorn and mule deer during some seasons. Given the relatively high number of concentrate selectors in CSP, white-tailed deer may be adapting to competition with these two species by consuming more graminoids.

MANAGEMENT IMPLICATIONS

We found potential competition and population trade-offs for the ungulate assemblage in CSP. Although each ungulate species followed *a priori* foraging strategies in agreement with Hoffman (1985), there is significant potential for competition among some species pairs during some seasons, especially elk and bison and white-tailed deer and elk. If managers aim to reduce or eliminate competition between the two principle foragers in the park, bison and elk, we recommend management actions that would increase the biomass of palatable cool-season and warm-season grasses, such as Kentucky bluegrass, western wheatgrass, and big bluestem. These actions would also facilitate elk and white-tailed deer coexistence, as would increases in shrub species such as leadplant and wild rose. Given the relatively high diversity of concentrate selectors in the park, monitoring of forage species that occur to a moderate extent in all 3 diets, including wild raspberry, wild rose, western snowberry, fringed sagewort, and cudweed sagewort, may be prudent to prevent overutilization.

In areas that support large diverse ungulate assemblages, significant dietary overlap may exist even when each species forages within their evolutionary niches. This may be especially true for small, closed reserves, or large reserves that support species that are typically nomadic or migratory. These data, in concert with data on ungulate resource selection, spatial overlap and spatially explicit forage production can be used to estimate carrying capacity of ungulate species in CSP.

LITERATURE CITED

Alipayo, D., R. Valdez, J. L. Holechek, and M. Cardenas. 1992. Evaluation of microhistological analysis for determining ruminant diet botanical composition. Journal of Range Management 45:148–152.

Bagchi, S., S. P. Goyal, and K. Sankar. 2003. Habitat separation among ungulates in dry tropical forests of Ranthambhore National Park Rajasthan. Tropical Ecology 44:177–183.

Bailey, J. A., and A. Y. Copperrider. 1982. Final Report: Trickle Mountain research study. United States Bureau of Land Mangement, Denver, Colorado, USA

Bayless, S. R. 1969. Winter food habits, range use, and home range of antelope in Montana. Journal of Wildlife Management 33:538–551.

Beck, J. L., and J. M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. Rangeland Ecology and Management 58:135–147.

Belovsky, G. E. 1997. Optimial foraging and community structure: the allometry of herbivore food selection and competition. Evolutionary Ecology 11:641–672.

Berger, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. Behavioral Ecology and Sociobiology 4:91–99.

Bodmer, R. E. 1991. Influence of digestive morphology on resource partitioning in Amazonian ungulates. Oecologia 85:361–365.

Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. Ecological Applications 16:1911–1925.

Christianson, D. A., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. Journal of Wildlife Management 71:164–176.

Cook, J. G. 2002. Nutrition and food. Pages 259–349 *in* North American elk: ecology and management. D. E. Toweill and J. W. Thomas, editors. Smithsonian Institute Press, Washington D.C., USA.

CSP. 1995. Custer State Park resource management plan 1995–2010. Unpublished document.

Davitt, B. B., and J. R. Nelson. 1980. A method of preparing plant epidermal tissue for use in fecal analysis. College of Agriculture Research Center, Washington State University, Pullman, Washington, USA.

Dearden, B. L., R. E. Pegau, and R. M. Hansen. 1975. Precision of microhistological estimates of ruminant habits. Journal of Wildlife Management 39:402–407.

Edge, W. D., C. L. Marcum, S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. The Journal of Wildlife Management 51:844–851.

Gibbs, M. C., J. J. Jenks, C. S. DePerno, B. F. Sowell, and K. J. Jenkins. 2004. Cervid forage utilization in noncommercially thinned ponderosa pine forests. Journal of Range Management 57:435–441.

Gordon, U., and A. W. Illius. 1989. Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383–389.

Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. Journal of Range Management 35:146–151.

Hansen, M. C., J. D. Yoakum, W. H. Pyle, and R. G. Anthony. 2001. New strategies for pronghorn food habit studies. Pronghorn Antelope Workshop Proceedings 19:71–94.

Herdandez, L., and J. W. Laundre. 2005. Foraging in the ‘landscape of fear’ and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. Wildlife Biology 11:215–220.

Hobbs, N. T., D. L. Baker, and R. B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. Journal of Wildlife Management 47:1–16.

Hofmann, R. R. 1985. Digestive physiology of the deer: their morphophysiological specialization and adaptation. Pages 393–407 *in* Biology of Deer Production. P. F. Fennessy, and K. R. Drew, editors. Royal Society of New Zealand, Wellington, New Zealand.

Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. Journal of Range Management 35:309–315.

Holechek, J. L., and R. Valdez. 1985. Magnification and shrub stemmy material influences on fecal analysis accuracy. Journal of Range Management 38:350–352.

Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56:989–999.

Jenks, J. A., D. M. Leslie, Jr., R. L. Lochmiller, M. A. Melchiors, and W. D. Warde. 1989. Effect of compositing samples on analysis of fecal nitrogen. Journal of Wildlife Management 53:213–215.

Jenkins, K. J., and R. G. Wright. 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. Canadian Journal of Zoology 65:1397–1401.

Jiang, G., M. Zhang, and J. Ma. 2007. Effects of human disturbance on movement, foraging, and bed selection in red deer (*Cervus elaphus* xanthopygus) from the Wandashan Mountains, northeastern China. Acta Theriologica 52:435–446.

Jones, D. I., and A. D. Wilson. 1987. Nutritive quality of forage. Pages 65–89 *in* J. B. Hacker and J. H. Ternouth, editors. The nutrition of herbivores. Academic Press, Sidney, Austrailia.

Keller, B. J., and J. J. Millspaugh. 2010. A forage allocation model for Wind Cave National Park. Final report submitted to Wind Cave National Park, Hot Springs, South Dakota.

Kingery, J. L., J. C. Mosely, and K. C. Bordwell. 1996. Dietary overalp among cattle and cervids in northern Idaho forests. Journal of Range Management 49:8–15.

Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota State University, College of Agriculture and Biological Sciences, South Dakota Agricultural Experiment Station, Brookings, South Dakota, USA.

Leuthold, W. 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35:241–252.

McCullough, Y. B. 1980. Niche separation of seven North American ungulates on the National Bison Range, Montana. Dissertation, University of Michigan, Ann Arbor, Michigan, USA.

Messenger, N. C., and F. Schitoskey. 1980. Components and digestibility of pronghorn diets. South Dakota Academy of Science 59:194–204.

Miller, W. 2002. Elk interactions with other ungulates. Pages 435–448 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and mangement. Smithsonian Institution Press, Washington D. C., USA.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994–1003.

Mitchell, G. J., and S. Smoliak. 1971. Pronghorn antelope range characteristics and food habits in Alberta. Journal of Wildlife Management 35:238–250.

Morris, M. S., and J. E. Schwartz. 1957. Mule deer and elk food habits on the National Bison Range. Journal of Wildilfe Management 21:189–193.

Murray, M. G., and A. W. Illius. 2000. Vegetative modification and resource competition in grazing ungulates. Oikos 89:501–508.

Prins, H. H., and H. Fritz. 2008. Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. Pages 179–200 *in* I. J. Gordon and H. H. Prins, editors. The ecology of browsing and grazing. Springer-Verlag, Berlin, Germany.

Profitt, K. M., J. L. Grigg, R. A. Garrott, K. L. Hamlin, J. Cunningham, J. A. Gude, and C. Jourdonnais. 2010. Changes in elk resource selection and distributions associated with a late-season elk hunt. The Journal of Wildlife Management 74:210–218.

Putnam, R. 1988. The natural history of deer. Cornell University press, Ithaca, New York, USA.

Putnam, R. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London, UK.

Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230:96–106.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. The Journal of Wildlife Management 65:899–914.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726.

Schoener, T. W. 1982. The controversy over interspecific competition. American Scientist 70:586–595.

Sievers, J. D. 2004. Factors influencing a declining pronghorn population in Wind Cave National Park, South Dakota. Thesis, South Dakota State University, Brookings, South Dakota, USA.

Singer, F. J., and J. E. Norland. 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canadian Journal of Zoology 72:1383–1394.

Skogland, T., and B. Grovan. 1988. The effects of human disturbance on the activity of wild reindeer in different physical condition. Rangifer 8:11–19.

Van Soest, P. J. 1994. Nutritional ecology of the ruminant. Cornell University Press, Ithaca, New York, USA.

Vavra, M., and J. L. Holechek. 1980. Factors influencing microhistological analysis of herbivore diets. Journal of Range Management 33:371–374.

Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–109 *in* L. K. Halls, editor. White-tailed deer. Stackpole Books, Mechanicsburg, Pennsylvannia, USA.

Wydeven , A. P. 1979. Food habits and ecological relationships of elk to other herbivores in Wind Cave National Park. Thesis, Iowa State University, Ames, Iowa, USA.

Wydeven, A. P., and Dahlgren, R. B. 1983. Food habits of elk in the northern Great Plains. Journal of Wildlife Management 47:916–923.

Wydeven, A. P. and Dahlgren, R. B. 1985. Ungulate habitat relationships in Wind Cave National Park. Journal of Wildlife Management 49:805–813.

Yoakum, J. D. 2004. Foraging ecology, diet studies and nutrient values. Pages 446–502 *in* B. W. O'Gara, and J. D. Yoakum, editors. Pronghorn ecology and management. University Press of Colorado, Boulder, Colorado, USA.

Zimmerman, T. J. 2004. Effects of fire on the nutritional ecology of selected ungulates in the southern Black Hills, South Dakota. Thesis, South Dakota State University, Brookings, South Dakota, USA.

Table 1. Number of slides read for microhistological analysis per ungulate species to determine seasonal diet composition in Custer State Park, South Dakota, 2005–2008.

Species	Fall	Winter	Spring	Summer	Total
Bison	44	38	41	77	200
Elk	26	25	31	57	139
Mule deer	23	10	7	10	50
White-tailed deer	38	29	31	39	137
Pronghorn	29	26	27	46	128

Table 2. Botanical (%) composition of bison diets in Custer State Park, SD, 2005–2008.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Andropogon geradii	4.9 (0.5)	5.0 (1.7)	3.7 (1.3)	3.0 (1.3)	4.1 (0.5)
Bouteloua gracilis	10.9 (1.3)	19.7 (1.2)	11.3 (4.1)	9.5 (1.0)	12.8 (2.3)
Bouteloua curtipendula	2.1 (1.6)	3.0 (1.9)	1.4 (1.0)	0.7 (0.2)	1.8 (0.5)
Bromus inermis	1.9 (0.3)	0.8 (0.4)	2.7 (0.8)	5.3 (1.3)	2.7 (1.0)
Bromus tectorum	1.6 (1.0)	1.3 (0.5)	1.6 (0.9)	0.3 (0.1)	0.8 (0.3)
Elymus canadensis	0.1 (0.1)	0.1 (0.1)	0.0	0.0	0.1 (0.1)
Calamovilfa longifolia	1.7 (1.4)	0.3 (0.3)	0.0	0.0	0.5 (0.4)
Carex spp.	22.2 (1.1)	18.3(3.8)	11.5 (2.8)	9.6 (1.9)	15.4 (2.9)
Danthonia spicata	0.4 (0.4)	0.5 (0.5)	0.9 (0.7)	0.0	0.4 (0.2)
Elymus elymoides	0.0	0.1 (0.1)	0.0	0.0	tr[e]
Muhlenbergia racemosa	0.0	0.7 (0.4)	0.4 (0.4)	0.2 (0.2)	0.7 (0.3)
Nassella viridula	1.7 (1.1)	1.9 (0.6)	2.6 (1.1)	2.7 (1.0)	2.2 (0.3)
Pascopyrum smithii	21.4 (5.3)	19.9 (3.5)	27.4 (6.4)	34.2 (3.0)	25.7 (3.3)
Phleum pratense	0.0	0.1 (0.1)	0.0	0.0	tr
Poa pratensis	17.0 (1.5)	15.4 (4.2)	26.8 (4.0)	20.0 (3.3)	19.8 (2.5)
Schizachyrium scoparium	1.8 (1.2)	2.5 (1.9)	1.3 (0.3)	2.4 (1.7)	2.0 (0.3)
Sporobolus cryptandrus	0.0	1.4 (1.2)	0.0	0.3 (0.3)	0.4 (0.3)
Stipa comata	6.9 (0.5)	5.5 (0.6)	5.1 (2.5)	3.6 (0.2)	5.3 (0.7)
Unknown Grass	0.0	0.0	0.4 (0.4)	0.2 (0.2)	tr
Total Grasses	94.6	96.5	97.1	92.0	94.7

Table 2, Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Amorpha canescens	0	0.1 (0.1)	0	1.9 (0.5)	0.5 (0.5)
Pinus ponderosa	0.5 (0.5)	0.4 (0.4)	0.4 (0.3)	0	0.7 (0.3)
Rosa spp.	0.3 (0.3)	0	0	2.0 (0.9)	0.6 (0.5)
Rubus idaeus	0	0.1 (0.1)	0	0.2 (0.2)	0.1 (0.1)
Symphoricarpus albus	0	0	0	0.2 (0.2)	tr
Unknown Shrubs	0.2 (0.2)	0	0.3 (0.3)	0.5 (0.3)	0.2 (0.1)
Total Shrubs	1	0.6	0.7	4.8	2.1
Artemisia ludoviciana	0.0	0.0	0.5 (0.3)	0.4 (0.4)	0.2 (0.1)
Unknown Forbs	4.3 (2.6)	3.1 (0.8)	1.7 (0.9)	1.4 (0.6)	2.7 (0.7)
Total Forbs	4.3	3.1	2.2	1.8	2.8

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30

[d]Winter = December 1–Feburary 28, [e] tr = trace amount (< 0.1 g)

Table 3. Botanical (%) composition of elk dietse in Custer State Park, SD, 2005-2008.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Andropogon geradii	4.8 (1.5)	3.0 (0.6)	5.0 (0.7)	1.7 (0.5)	3.6 (0.8)
Bouteloua curtipendula	0.6 (0.4)	0.8 (0.4)	0.0	0.3 (0.3)	0.4 (0.2)
Bouteloua gracilis	2.1 (0.2)	9.5 (1.1)	2.9 (1.3)	1.2 (0.9)	3.9 (1.9)
Bromus inermis	4.3 (1.8)	0.7 (0.7)	1.3 (0.4)	3.9 (1.0)	2.5 (0.9)
Bromus tectorum	1.8 (1.3)	0.6 (0.3)	0.6 (0.4)	0.0	0.7 (0.4)
Carex spp.	20.1 (8.0)	12.4 (1.6)	10.8 (1.9)	3.8 (1.6)	11.8 (3.3)
Nassella viridula	0.2 (0.2)	1.2 (0.8)	2.6 (1.5)	0.5 (0.3)	1.1 (0.5)
Pascopyrum smithii	10.8 (0.8)	7.4 (2.2)	11.5 (3.1)	15.2 (6.0)	11.2 (1.6)
Poa pratensis	30.4 (11.2)	10.1 (1.8)	21.3 (4.8)	32.8 (2.0)	23.6 (5.2)
Schizachyrium scoparium	0.8 (0.5)	2.4 (0.8)	2.3 (0.5)	2.0 (0.8)	1.9 (0.4)
Stipa comata	5.2 (1.8)	0.6 (0.6)	1.5 (0.6)	2.0 (0.6)	2.3 (1.0)
Unknown Grass	0.2 (0.2)	0.2 (0.2)	0.0	0.0	0.1 (0.1)
Total Grasses	81.3	48.9	59.8	63.4	63.1
Amorpha canescens	3.6 (2.8)	9.5 (9.0)	5.3 (2.8)	0.2 (0.2)	4.6 (1.9)
Arctostaphylus uva-ursii	0.0	0.0	3.6 (3.6)	2.1 (1.7)	1.4 (0.9)
Cercocarpus montanus	0.0	0.3 (0.3)	0.9 (0.9)	0.9 (0.5)	0.5 (0.2)

Table 3. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Pinus ponderosa	2.5 (1.6)	1.7 (1.0)	2.0 (1.0)	13.8 (3.0)	5.0 (2.9)
Quercus spp.	0.0	0.8 (0.4)	0.4 (0.2)	0.3 (0.3)	0.4 (0.2)
Rhus aromatica	0.0	0.1 (0.1)	0.9 (0.4)	0.0	0.3 (0.2)
Rosa spp.	1.0 (0.8)	9.2 (3.7)	3.4 (1.0)	0.5 (0.5)	3.5 (2.0)
Rubus idaeus	1.0 (0.5)	0.9 (0.5)	0.2 (0.2)	0.0	0.5 (0.2)
Symphoricarpus albus	1.7 (1.7)	5.5 (5.2)	2.4 (1.6)	0.7 (0.4)	2.6 (1.1)
Unknown Shrubs	2.8 (2.4)	1.5 (1.5)	11.4 (2.5)	11.8 (3.2)	6.9 (2.7)
Total Shrubs	12.6	29.5	30.5	30.3	25.7
Achillea millefolium	0	3.2 (2.2)	0.4 (0.4)	1.3 (0.3)	1.3 (0.7)
Antennaria spp.	0.2 (0.2)	0	0	0	0.1 (0.1)
Apocynum androsaemifolium	0.3 (0.3)	0.7 (0.7)	0	0	0.3 (0.2)
Artemisia frigida	0	0.3 (0.3)	0	0.2 (0.2)	0.1 (0.1)
Artemisia ludoviciana	0.7 (0.4)	0.4 (0.2)	0.9 (0.6)	0.5 (0.3)	0.6 (0.1)
Asclepias pumila	0	0.1 (0.1)	0	0	tr
Campanula rotundifolia	0	0.3 (0.3)	0	0	0.1 (0.1)
Cirsium spp.	0	0.1 (0.1)	0	0	tr

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g).

Table 3. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Fragaria virginiana	0.2 (0.2)	0.0	0.0	0.0	0.1 (0.1)
Galium boreale	0.0	0.0	0.4 (0.4)	0.5 (0.5)	0.2 (0.1)
Monarda fistulosa	0.0	0.1 (0.1)	0.2 (0.2)	0.0	0.1 (0.1)
Plantago patagonica	0.0	0.0	0.0	0.2 (0.2)	0.1 (0.1)
Sisyrinchium montanum	0.0	0.1 (0.1)	0.0	0.0	tr
Solidago spp.	0.0	0.7 (0.5)	0.0	0.0	0.2 (0.2)
Verbascum thapsus	0.0	0.5 (0.5)	0.0	0.0	0.1 (0.1)
Unknown Forbs	4.2 (2.5)	14.6 (6.9)	6.5 (3.7)	2.4 (1.7)	6.9 (2.7)
Total Forbs	5.6	21.1	8.4	5.1	10.2

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 4. Botanical (%) composition of pronghorn diets in Custer State Park, SD, 2005-2008.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Andropogon geradii	1.3 (1.3)	1.0 (0.7)	1.0 (0.5)	0.0	0.8 (0.3)
Bouteloua gracilis	0.4 (0.4)	0.9 (0.5)	0.0	0.0	0.3 (0.2)
Bromus inermis	1.0 (0.8)	0.2 (0.2)	0.6 (0.3)	0.6 (0.6)	0.6 (0.2)
Carex spp.	1.7 (1.1)	1.0 (0.7)	0.3 (0.3)	0.0	0.8 (0.4)
Nassella viridula	1.2 (0.8)	0.3 (0.3)	0.0	0.0	0.4 (0.3)
Pascopyrum smithii	4.4 (2.5)	6.0 (1.4)	1.6 (1.6)	1.2 (0.3)	3.3 (1.2)
Poa pratensis	6.4 (3.1)	2.6 (0.9)	3.9 (2.0)	1.2 (0.5)	3.5 (1.1)
Schizachyrium scoparium	0.1 (0.1)	0.0	0.2 (0.2)	0.0	tr
Stipa comata	0.3 (0.3)	0.0	0.0	0.0	0.1 (0.1)
Total Grasses	16.8	12.0	7.6	3.0	9.8
Amorpha canescens	8.3 (3.2)	7.0 (3.3)	1.9 (0.3)	9.1 (2.8)	6.6 (1.6)
Juniperus communis	0.0	0.1 (0.1)	0.0	0.0	tr
Pinus ponderosa	1.2 (0.5)	1.6 (1.4)	0.4 (0.3)	4.1 (2.8)	1.8 (0.8)
Rosa spp.	2.2 (1.6)	26.3 (3.3)	16.6 (1.2)	2.1 (0.9)	11.8 (5.9)
Rubus idaeus	3.0 (1.8)	4.2 (1.3)	4.0 (3.7)	2.0 (1.3)	3.3 (0.5)
Symphoricarpus albus	1.9 (1.2)	2.5 (2.1)	4.5 (1.7)	0.8 (0.1)	2.4 (0.8)
Unknown Shrubs	14.0 (3.4)	8.4 (1.1)	19.4 (3.7)	16.0 (0.4)	14.5 (2.3)
Total Shrubs	30.6	50.1	46.8	34.1	40.4

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 4. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Achillea millefolium	0.0	0.5 (0.5)	0.0	0.0	0.1 (0.1)
Artemisia frigida	45.2 (17.1)	7.6 (3.8)	34.8 (10.7)	57.7 (3.6)	36.3 (10.7)
Artemisia ludoviciana	0.6 (0.6)	10.3 (0.4)	5.3 (2.4)	1.0 (0.5)	4.3 (2.3)
Campanula rotundifolia	0.8 (0.5)	0.5 (0.5)	0.2 (0.2)	0.0	0.4 (0.2)
Plantago patagonica	0.7 (0.4)	1.4 (0.4)	1.9 (0.2)	0.0	1.0 (0.4)
Solidago spp.	0.0	0.0	0.2 (0.2)	0.0	tr
Trifolium spp.	0.0	0.4 (0.2)	2.1 (1.8)	0.0	0.6 (0.5)
Unknown Forbs	4.7 (4.5)	15.3 (3.5)	1.0 (0.5)	1.0 (0.5)	5.5 (3.4)
Total Forbs	52.0	36.0	45.5	59.7	48.2

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 5. Botanical composition (%) of white-tailed deer diets in Custer State Park, SD, 2005–2008.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Andropogon geradii	0.7 (0.4)	0.4 (0.4)	0.3 (0.3)	0.5 (0.5)	0.5 (0.1)
Bouteloua gracilis	0.2 (0.2)	0.2 (0.2)	0.0	0.3 (0.3)	0.2 (0.1)
Bromus inermis	0.8 (0.4)	1.8 (1.0)	0.7 (0.4)	4.0 (2.2)	1.8 (0.8)
Carex spp.	2.5 (1.2)	2.9 (1.2)	0.9 (0.7)	0.8 (0.5)	1.8 (0.5)
Muhlenbergia racemosa	0.0	0.1 (0.1)	0.0	0.0	tr
Nassella viridula	1.1 (0.5)	0.1 (0.1)	0.0	0.8 (0.8)	0.5 (0.3)
Pascopyrum smithii	10.0 (7.6)	3.8 (1.5)	5.9 (1.5)	2.2 (1.0)	5.5 (3.4)
Poa pratensis	18.9 (7.1)	15.0 (5.1)	14.4 (0.1)	18.3 (2.7)	16.7 (2.3)
Schizachyrium scoparium	0.2 (0.2)	0.1 (0.1)	0.0	1.1 (1.1)	0.4 (0.3)
Sporobolus cryptandrus	0.0	0.1 (0.1)	0.0	0.0	tr
Stipa comata	0.5 (0.3)	1.5 (0.8)	0.3 (0.3)	1.7 (1.0)	1.0 (0.4)
Unknown Grass	0.8 (0.8)	0.0	0.3 (0.3)	0.2 (0.2)	0.3 (0.2)
Total Grasses	35.7	26.0	22.8	26.4	28.7

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 5. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Amorpha canescens	3.4 (2.5)	5.4 (3.1)	0.3 (0.3)	0.5 (0.3)	2.4 (1.2)
Arctostaphylus uva-ursii	0.0	0.0	0.0	5.5 (3.7)	1.4 (1.4)
Juniperus communis	0.0	0.1 (0.1)	0.0	0.8 (0.8)	0.2 (0.2)
Pinus ponderosa	20.4 (15.5)	2.3 (0.6)	5.4 (2.7)	43.4 (1.0)	17.9 (9.4)
Populus tremmuloides	0.1 (0.1)	0.4 (0.4)	0.0	0.0	0.1 (0.1)
Prunus virginiana	0.0	0.4 (0.4)	0.0	0.3 (0.3)	0.2 (0.1)
Quercus spp.	0.0	0.2 (0.2)	2.3 (1.7)	0.2 (0.2)	0.7 (0.5)
Rhus aromatica	0.0	0.4 (0.4)	1.5 (1.3)	0.0	0.5 (0.4)
Rosa spp.	3.6 (2.4)	20.2 (9.2)	17.4 (3.2)	3.8 (3.0)	11.3 (4.4)
Rubus idaeus	10.0 (9.7)	7.3 (4.0)	11.5 (5.4)	0.0	7.2 (2.6)
Symphoricarpus albus	1.4 (1.2)	5.2 (1.9)	9.7 (3.1)	3.1 (1.5)	4.9 (1.8)
Unknown Shrubs	8.2 (4.2)	6.8 (0.6)	8.9 (1.0)	9.3 (1.5)	8.3 (0.6)
Total Shrubs	47.1	48.7	57.0	66.9	55.1
Achillea millefolium	2.2 (1.8)	4.5 (0.9)	0.6 (0.5)	1.1 (0.6)	2.1 (0.9)
Antennaria spp.	0.0	0.2 (0.2)	0.0	0.0	tr
Apocynum androsaemifolium	0.0	0.2 (0.2)	0.0	0.0	tr

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 5. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Artemisia frigida	0.7 (0.4)	0.3 (0.2)	0.2 (0.2)	0.0	0.3 (0.2)
Artemisia ludoviciana	0.4 (0.4)	2.8 (1.2)	5.8 (1.6)	0.2 (0.2)	2.3 (1.3)
Campanula rotundifolia	0.1 (0.1)	0.9 (0.6)	0.2 (0.2)	0.2 (0.2)	0.4 (0.2)
Cirsium spp.	0.0	0.0	0.2 (0.2)	0.0	tr
Echinacea purpurea	0.0	0.2 (0.2)	0.0	0.0	tr
Fragaria virginiana	0.1 (0.1)	0.0	0.0	0.0	tr
Galium boreale	0.3 (0.2)	0.0	0.1 (0.1)	0.0	0.1 (0.1)
Liatris spp.	0.0	0.1 (0.1)	0.0	0.0	tr
Monarda fistulosa	0.1 (0.1)	0.0	0.1 (0.1)	0.0	tr
Plantago patagonica	0.9 (0.8)	0.7 (0.1)	0.6 (0.4)	0.0	0.6 (0.2)
Solidago spp.	0.0	0.1 (0.1)	1.0 (0.3)	0.0	0.3 (0.2)
Trifolium spp.	2.1 (2.1)	1.4 (0.7)	3.6 (2.2)	0.0	1.8 (0.8)
Verbascum thapsus	0.6 (0.6)	0.8 (0.8)	0.5 (0.3)	0.0	0.5 (0.2)
Unknown Forbs	9.7 (4.3)	11.4 (5.7)	6.3 (3.0)	0.8 (0.1)	7.1 (2.3)
Total Forbs	17.2	23.6	19.2	2.3	16.2

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 6. Botanical compsition (%) of mule deer diets in Custer State Park, SD, 2005-2008.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Andropogon geradii	0.0	0.0	0.2 (0.2)	0.0	tr
Bromus inermis	0.0	0.0	0.4 (0.4)	0.0	0.1 (0.1)
Carex spp.	0.0	0.0	0.2 (0.2)	0.0	0.1 (0.1)
Nassella viridula	0.0	0.0	0.6 (0.6)	0.0	0.2 (0.2)
Pascopyrum smithii	0.4 (0.4)	0.9 (0.9)	2.2 (1.2)	0.0	0.9 (0.5)
Poa pratensis	1.8 (1.2)	4.1 (2.4)	1.8 (0.9)	3.5 (0.9)	2.8 (0.6)
Schizachyrium scoparium	0.0	0.4 (0.4)	0.0	0.6 (0.6)	0.3 (0.2)
Stipa comata	0.0	0.0	0.0	0.6 (0.6)	0.1 (0.1)
Total Grasses	2.2	5.4	5.4	4.7	5.1
Amorpha canescens	21.5 (8.5)	15.4 (11.7)	1.6 (0.9)	21.5 (3.2)	15.0 (6.7)
Arctostaphylus uva-ursii	0.0	0.0	0.4 (0.4)	2.0 (1.3)	0.6 (0.5)
Juniperus communis	0.0	0.0	0.4 (0.2)	0.0	0.1 (0.1)

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 6. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Pinus ponderosa	23.5 (8.0)	2.2 (2.2)	2.2 (1.9)	18.3 (2.6)	11.6 (5.5)
Quercus spp.	0.0	0.0	2.6 (2.0)	0.0	0.7 (0.7)
Rhus aromatica	0.0	0.0	0.2 (0.2)	0.0	0.1 (0.1)
Rosa spp.	7.5 (4.3)	35.8 (12.7)	10.3 (5.2)	1.3 (0.7)	13.7 (7.6)
Rubus idaeus	5.0 (5.0)	1.3 (1.3)	6.7 (3.7)	4.3 (1.4)	4.2 (1.0)
Symphoricarpus albus	4.4 (1.6)	28.3 (5.0)	21.2 (3.0)	2.2 (1.3)	14.1 (6.4)
Unknown Shrubs	20.0 (4.9)	3.9 (3.9)	6.1 (3.3)	20.6 (4.3)	12.6 (4.4)
Total Shrubs	81.9	86.9	51.7	70.2	72.7
Achillea millefolium	1.7 (1.7)	0.0	0.0	1.1 (1.1)	0.7 (0.4)
Artemisia frigida	12.5 (8.0)	0	8.9 (5.6)	21.7 (3.6)	10.8 (4.5)
Artemisia ludoviciana	0	6.7 (0.1)	19.6 (4.6)	1.3 (0.7)	6.9 (4.5)
Galium boreale	0.0	0.0	0.2 (0.2)	0.0	0.1 (0.1)
Plantago patagonica	0.8 (0.8)	0.4 (0.4)	0.8 (0.8)	0.0	0.5 (0.2)
Solidago spp.	0.0	0.0	7.5 (6.3)	0.0	1.9 (1.9)

[a]Spring = March 1–May 31, [b]Summer = June 1–August 31, [c]Fall = September 1–November 30, [d]Winter = December 1–Feburary 28, [e]tr = trace amount (< 0.1 g)

Table 6. Continued.

Species	Spring[a]	Summer[b]	Fall[c]	Winter[d]	Overall
Trifolium spp.	0.0	0.0	0.4 (0.2)	0.0	0.1 (0.1)
Verbascum thapsus	0.0	0.0	1.6 (1.6)	0.0	0.4 (0.4)
Unknown Forbs	0.8 (0.8)	0.0	3.8 (1.6)	1.3 (0.7)	1.5 (0.8)
Total Forbs	15.8	7.1	42.8	25.4	22.9

[a] Spring = March 1–May 31, [b] Summer = June 1–August 31, [c] Fall = September 1–November 30, [d] Winter = December 1–Feburary 28, [e] tr = trace amount (< 0.1 g)

Table 7. Schoener's (1968) dietary overlap index (1 = complete overlap. 0 = complete separation) among ungulate species in Custer State Park, SD, based on microhistological analysis of ungulate feces, 2005–2008.

Season	Species	Bison	Elk	Pronghorn	White-tailed deer
Spring	Elk	0.706			
	Pronghorn	0.225	0.325		
	White-tailed deer	0.384	0.513	0.420	
	Mule deer	0.041	0.159	0.472	0.483
Summer	Elk	0.526			
	Pronghorn	0.166	0.520		
	White-tailed deer	0.295	0.606	0.675	
	Mule deer	0.062	0.347	0.545	0.477
Fall	Elk	0.611			
	Pronghorn	0.099	0.299		
	White-tailed deer	0.262	0.500	0.516	
	Mule deer	0.084	0.277	0.478	0.556
Winter	Elk	0.551			
	Pronghorn	0.115	0.242		
	White-tailed deer	0.341	0.578	0.214	
	Mule deer	0.111	0.373	0.597	0.392

Table 7. Continued.

Season	Species	Bison	Elk	Pronghorn	White-tailed deer
Overall	Elk	0.630			
	Pronghorn	0.156	0.355		
	White-tailed deer	0.336	0.603	0.496	
	Mule deer	0.083	0.308	0.609	0.548

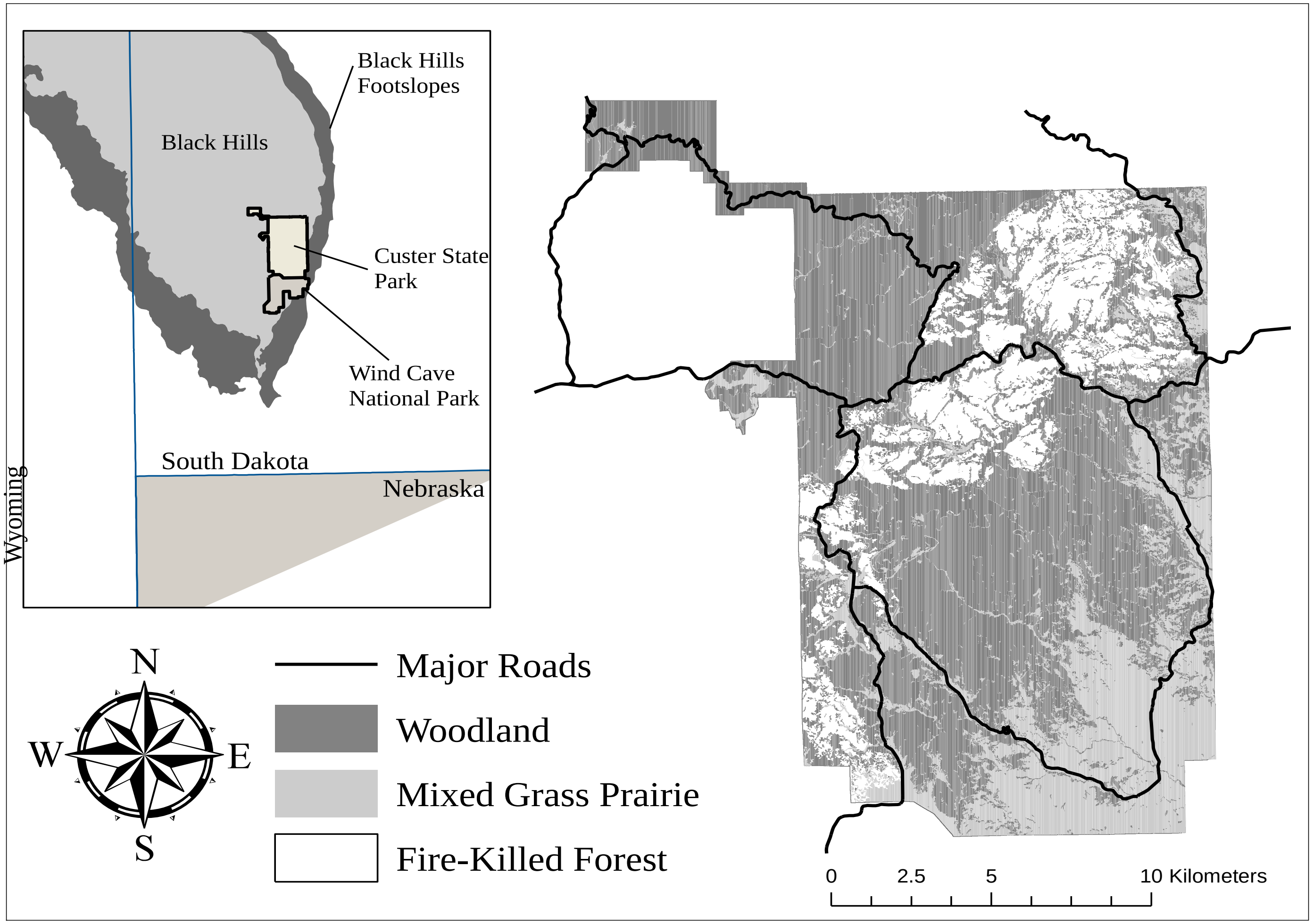

Figure 4. Major habitat types and features of Custer State Park, SD.

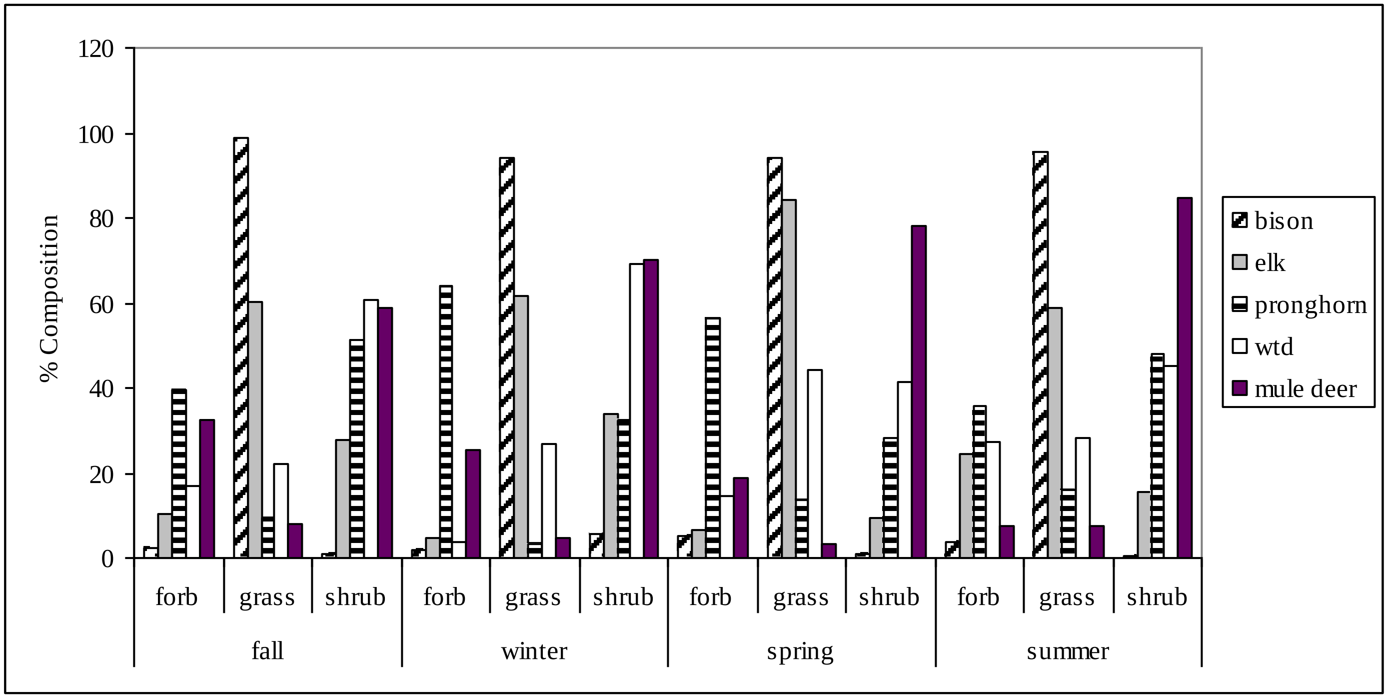

Figure 2. Seasonal diet composition (%) of ungulate species in Custer State Park, SD, based on data collected 2005-2008.

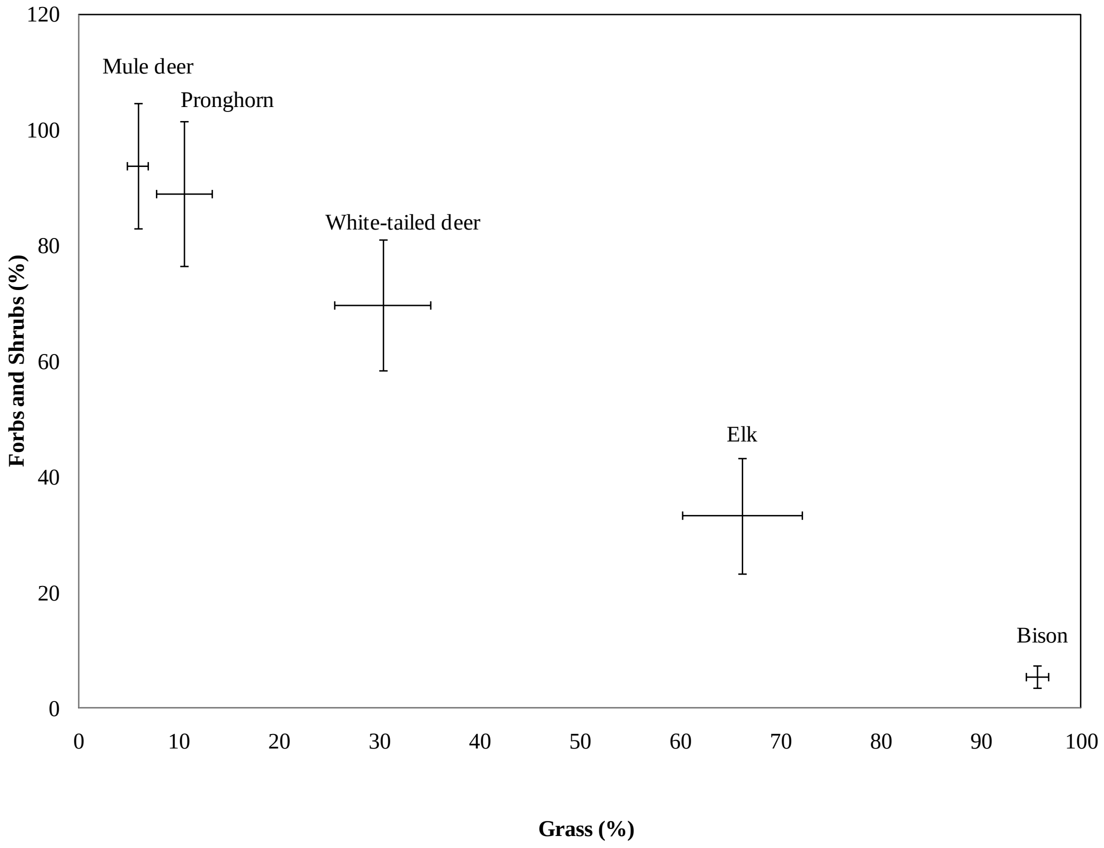

Figure 3. Breadth of seasonal composition (95% confidence interval for average composition) of grass and forb and shrub species in ungulate diets in Custer State Park, SD, 2005-2008.

CHAPTER V. ANALYSIS OF FACTORS INFLUENCING HABITAT OVERLAP AMONG AN UNGULATE ASSEMBLAGE IN THE BLACK HILLS, SOUTH DAKOTA

ABSTRACT

Interspecific spatial overlap can influence survival, resource selection, and range carrying capacity of ungulate assemblages; however, relatively little is known about why overlap occurs where it does on the landscape. We evaluated habitat overlap among an ungulate assemblage in Custer State Park, South Dakota, and assessed *a priori* hypotheses regarding mechanisms driving spatial heterogeneity in interspecific overlap. We used locations obtained from radio-tracking of bison (*Bison bison*), pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) to model habitat overlap. Using a classification tree, we assessed which habitat features most differentiated habitat use of the 5 species. We calculated an estimate of overlap based on the inability of the classification tree to separate use by the ungulate assemblage, projected this overlap index on the landscape, and ranked hypotheses about what was driving overlap in habitat use using a general linear model and an information theoretic approach. Habitat overlap among all species was highest during winter and lowest during the summer. Female bison and pronghorn, both sexes of bison and elk, and white-tailed deer and elk used habitat in a similar manner during most seasons. For all seasons except summer, habitat overlap was most associated with high forage biomass and water at the edges of habitat patches. During fall and winter, habitat overlap among all species increased at areas of

high forage biomass and diversity and areas of high patch edge density. During spring, habitat overlap among all species increased near intermittent streams at areas of high patch edge density. During summer high habitat overlap among all species was found close to intermittent streams, and away from flowing streams and ponds. Our data are consistent with the hypothesis that coevolutionary divergence or competition has resulted in habitat partitioning among the ungulate assemblage, with overlap among ungulates occurring at high quality resources within these habitat edges.

INTRODUCTION

Interspecific spatial interactions can have a substantial impact on the survival, behavior, fitness and resource selection of an organism (Matsuda et al. 2003, Gurevitch et al. 2000, Lynch and Rochette 2009). Spatial overlap may promote exploitative competition (i.e., utilization of the same resources in short supply) or interference competition (i.e., aggression between two species; Case and Gilpin 1974, Schoener 1983). Exploitative competition among sympatric ungulates is hypothesized to be minimal due to the evolutionary process of niche development (Schoener 1974, Putnam 1988). Empirical evidence supports this hypothesis (Schwartz and Ellis 1981, Hanley 1984, Putnam 1986, Jenkins and Wright 1988, Avey et al. 2003). However, because ungulate populations rarely exist in “natural” conditions, given limited emigration and immigration due to fences, absence of large predators, and removal of preferred habitat for many ungulate populations, the potential for competition may be increased as species may be forced to temporarily subsist outside of their evolutionary niches (Putnam 1988, Bagchi et al. 2003). Resource competition may also vary under seasonal climate variability. In general, there is an increase in competitive potential during periods of resource limitation such as winter months and drought years (Wydeven and Dahlgren 1985, Jenkins and Wright 1988, Putnam 1988). Thus, complete niche separation rarely exists in the natural environment (Putnam 1996) and proper management of resources for ungulates relies on understanding where and when overlap, and thus competition, may be occurring.

While studies describing the amount of habitat overlap and potential competition among ungulate assemblages are common in the literature (Wydeven and Dahlgren 1985, Ben-Shahar and Skinner 1988, Jenkins and Wright 1988, Dublin et al. 1990, Putnam 1996, Shrestha and Wegge 2008), few studies attempt to address the mechanisms behind overlap. Studies tend to quantify percent overlap among home ranges (Chapman et al. 1993, Ilse and Hellgren 1995, Keuroghlian et al. 2004, Brunjes et al. 2009) or distributions (Barrett 1982, Wood 1989, Latham et al. 1997), or describe areas where species overlap (Wydeven and Dahlgren 1985, Cobb et al. 2004, Coe et al. 2005, Shrestha and Wegge 2008). There has been no attempt to test hypotheses about why overlap occurs where it does, which is the main mechanism by which we gain reliable knowledge (Romesburg 1981) in wildlife science. While descriptions of areas where species overlap are crucial to the manager of that particular study area to prevent detrimental impacts to both wildlife and habitats, identifying the mechanisms influencing overlap among species provides information of much broader scientific and management relevance. Hypotheses about mechanisms can be tested by examining factors associated with spatial heterogeneity in overlap within an information-theoretic approach (Burnham and Anderson 1998).

Based on the available literature, several hypotheses emerge regarding features important to the spatial distribution of individual ungulates, and therefore potentially important to their spatial overlap. Habitat overlap among competing organisms may be concentrated at critical resources that promote survival or reproductive potential. For ungulates, these might include areas of high forage quality or quantity, or areas that provide contact with conspecifics and facilitate predator avoidance. Streams and watering holes may affect overlap indirectly due to the forage characteristics of these areas or directly as water sources (McNaughton 1990, Gaylord et al. 2003). Topographic features that influence forage quality or quantity (Dix 1958, Nellemann and Thomsen 1994) or that decrease risk of predation (Lingle 2002, Ripple and Beschta 2004) may also be important areas for spatial overlap. Human disturbance might be perceived as predation risk by prey species (Frid and Dill 2002) and thus areas that minimize human disturbance, including areas far from roads and human activity, may be important for a number of ungulate species. Thermoregulatory cover, although unlikely to directly increase survival or fitness (Cook et al. 1998), may nonetheless be an important resource for large temperate ungulates such as elk (*Cervus elaphus*; Millspaugh et al. 1998, Ager et al. 2003) and bison (*Bison bison*; Maichek et al. 2004) that may seek out areas that alleviate heat stress during the summer.

Interspecific spatial overlap is likely to increase with the number of species in a system, especially if any of the species are habitat generalists with broad niches. In coevolutionary species assemblages, overlap on one dimension of resource use (spatial or diet) implies separation on the other dimension (Schoener 1974). In communities with a large number of sympatric ungulate species, niche development may lead to dietary divergence allowing high spatial overlap, divergence in the spatial niche when diet overlap is high, or a combination of both. Thus, spatial overlap may not be associated with high quality resources but rather spatial patch boundaries. Habitat edges may be the first to receive overlap pressure as populations increase or habitat quality diminishes due to seasonal climatic fluctuations or disturbance. Within these patch edges we would expect animals to interact at critical resources, such as food and water.

Custer State Park, located in the Black Hills of South Dakota, supports populations of 5 sympatric ungulate species: bison, elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and pronghorn (*Antilocapra americana*). These are primarily ‘closed’ populations as a fence surrounds the majority of the park and prevents or limits dispersal of ungulate populations. Further, populations of wolves (*Canis lupus*) and grizzly bear (*Ursus arctos horribilis*) native to the ecosystem have been extirpated. These conditions likely deviate from those in which the assemblage evolved to exist, and thus interspecific niche overlap may be expected to be high among the ungulate assemblage. Custer State Park thus provides a unique opportunity to test hypotheses about why overlap occurs among the assemblage on the landscape. Our objectives were to 1) estimate habitat overlap among sympatric ungulates; 2) depict spatially where overlap occurred; and 3) test hypotheses about factors affecting interspecific habitat overlap in Custer State Park.

STUDY AREA

Custer State Park encompasses 286.32 km^2 in southwest South Dakota, approximately 27 km southwest of Rapid City. Custer State Park is composed of a mixture of rangeland and forest common to the southern Black Hills region. Steep granite spires characterize the northwest portion of the Park, undulating forested hills dominate the central portion, and grasslands dominate the eastern and southern portions of the Park (CSP 1995; Figure 1). Elevations range from 1,146–2,042 meters (CSP 1995).

Over half (55%) of CSP is covered by forest. The central forested portion of CSP is dominated by ponderosa pine (*Pinus ponderosa*) which shifts to a mixture of ponderosa pine and white spruce (*Picea glauca*) on northern slopes and high elevations (Figure 1). A small amount of deciduous forest (2% of CSP) is characterized by predominantly bur oak (*Quercus macrocarpa*) and paper birch (*Betula papyrifera*) forest occurs primarily in riparian corridors (Figure 1). Stand structure diversity in CSP consists of 52.33 km^2 of single-story forest and 71.49 km^2 of multi-story forest (CSP 1995). Woodland understory communities in CSP are dominated by Kentucky bluegrass (*Poa pratensis*), poverty oatgrass (*Danthonia spicata*), sedges (*Carex* spp.), bearberry (*Arctostaphylos uva-ursi*), wild raspberry (*Rubus ideaus*), and western snowberry (*Symphoicarpus occidentalis*; Custer State Park, unpublished data). Almost 30% of CSP is burned-over forest, the results of the Galena fire of 1988, the Cicero Peak fire of 1990, and the Four-mile fire of 2008. Fire-damaged forest consists of 109.79 km^2, 60% of which is fire-killed where nominal regeneration has occurred and where the canopy remains open (CSP 1995; Figure 1).

Approximately 21% (61.05 km^2) of CSP is northern mixed-grass prairie and upland shrubland (CSP 1995; Figure 1). Grasslands are dominated by Kentucky bluegrass, big bluestem (*Andropogen gerardi*), little bluestem (*Andropogen scoparius*), western wheatgrass (*Agropyron smithi*), blue grama (*Bouteloua gracilis*), and sideoats grama (*Bouteloua curtipendula*; CSP 1995). Common shrub species include leadplant (*Amorpha canscens*), western snowberry, wild raspberry, and wild rose (*Rosa* spp.). Approximately 28,499,216 kg of palatable forage is produced in an average year in CSP (Chapter 1).

Thirteen watersheds occur either completely or partially within the Park (CSP 1995). There were 6 streams with constant annual flow and numerous ephemeral and permanent water impoundments in CSP during our study period (Figure 1). Water impoundments were created in the prairie region specifically for use by bison and other wildlife, or were already present when CSP was created from old ranching operations. Four large reservoirs are present in CSP, although two of these are outside of the fenced portion of the park and unavailable to bison. The other two reservoirs are located outside of the prairie region. There were two solar-driven water troughs located in the prairie region during the study period that provided a constant supply of fresh water for wildlife, and 69 other small permanent and ephemeral ponds. The maximum and average distance to a water source in CSP was 2.73 and 0.69 km, respectively.

For 1992–2008, annual precipitation for CSP averaged 49.86 cm and ranged from 74% to 161% of the 25-year mean. Approximately 76% of precipitation in CSP fell from April to September (Custer State Park, unpublished data). Winter in the southern Black Hills is considerably milder than elsewhere in the region, and a persistent snowpack was not typically present during the study period. Average snowfall for the southern Black Hills is 32.0 cm; March is the snowiest month with an average snowfall of 18.8 cm. Temperatures in CSP are more moderate than the surrounding plains; the average annual,

summer and winter temperature in CSP is 6.7° C, 16° C, and –5° C, respectively (CSP 1995).

Approximately 800–1000 bison, 408–1126 elk, 98–279 pronghorn, 867 white-tailed deer, 285 mule deer, 38–200 bighorn sheep, and 35–40 feral burros (*Equus asinus*) occupied CSP during our study period (C. Lehman, Custer State Park, personal communication). Bison are culled annually during the fall bison roundup, as well as during several hunts in the fall. Coyotes (*Canis latrans*), mountain lions (*Felis concolor*) and bobcats (*Felis rufus*) are the major predators in CSP. Wolves (*Canis lupus*) and grizzly bear (*Ursus arctos*) populations native to the region have been extirpated. A 1.54 m woven-wire fence surrounds the majority of the CSP except for a small portion of the Park in the Needles and Sylvan Lake area. This fence prevents movement of bison but allowed for movement of all other ungulate species into or out of CSP, although movement of ungulates out of the park is rare (CSP, unpublished data). There are three other internally fenced areas in CSP, which create three distinct pastures in CSP and are used to move bison during the roundup and to manage grazing of bison throughout the year (Figure 1).

There is a considerable amount of human-related infrastructure in CSP, consisting of paved, gravel, and two track roads and numerous buildings and campgrounds. There are 90.1 km of paved roads, including two state highways, and 76.5 km of gravel roads open to the public, in CSP. Two-track roads, that are only used by park employees, cover 560.9 km. There are approximately 84 small structures and buildings in the park, six campgrounds, and one small airport. From 2005–2008, an average of 1,631,432 people visited CSP annually. The majority of this visitation (59%) occurred during the summer, followed by fall (20%), spring (16%) and winter (5%; C. Pugsley, Custer State Park, personal communication).

METHODS

Radiotelemetry

We used radio-telemetry to examine resource use of all ungulate species in CSP. We used elk location data from Millspaugh (1999) and white-tailed deer and mule deer location data from Woeck (2003). These data were obtained during separate studies of elk and deer resource selection in CSP. Elk location data were gathered from September 1993- September 1997. Twenty-eight adult elk (9 males [M], 19 females [F]) were captured using modified Clover traps (Thompson et al. 1989) and helicopter netgunning (Millspaugh 1999). Description of capture and immobilization was provided in Millspaugh (1999). Captured elk were fitted with a mortality sensing radio-collar, ear-tagged, and subsequently released. Millspaugh (1999) located elk using ground telemetry techniques to acquire most (>95%) locations of radiocollared elk (Mech 1983, White and Garrott 1990) as well as aircraft with dual side-looking 4-element Yagi (Cushcraft, Keene, NH, USA) or 2-element H-antennas (Telonics, Mesa, AZ, USA) for the remaining 5%, using methodology described by Mech (1983). Ground tracking used the loudest signal method (Springer 1979) and triangulation techniques (Mech 1983). The computer program XYLOG (Dodge and Steiner 1986) was used to estimate elk locations by triangulation. Millspaugh (1999) recorded a total of 10,042 elk locations that we used for analysis.

Deer location data were gathered from May 2000-August 2002. Twenty-three white-tailed deer (11 M, 12 F) and 17 mule deer (7 M, 10 F) were captured via Clover traps (Clover 1954). Description of capture immobilization was provided in Woeck (2003). Deer were fitted with mortality-sensing radio-collars (AVM Instrument Co., Ltd., Livermore, CA; Lotek Engineering, Inc., Newmarket, Ontario, CA), ear-tagged, and released. Clover traps were placed throughout CSP to ensure adequate sampling of both deer and elk populations. White-tailed deer and mule deer were located approximately 5 times per week, May-August 2000, January–July 2001 and January–July 2002. CSP personnel located deer at least once every month September–December 2000 and August–December 2001. Woeck (2003) used the loudest signal method (Springer 1979) to estimate deer locations with a minimum of 3 compass bearings within 15 minutes. Woeck (2003) used the program GTM (Sartwell 2000) to estimate UTM locations from triangulation data. Woeck (2003) recorded a total of 2879 white-tailed deer and 2416 mule deer locations that we used for analysis.

To augment our historical data, we undertook a multi-year study of bison and pronghorn habitat use. We monitored 35 bison (25 females and 10 males) from October 2005 - August 2008. We radio-collared 24 female bison during the annual fall bison roundup in October 2005. All female and juvenile male bison (generally less than 4 years in age) were moved into a holding pen during the roundup and separated using a modified cattle chute system. We placed radio-collars equipped with mortality sensors (Advanced Telemetry Systems, Isanti, MN, USA) around the necks of adult females as we caught them in the squeeze chute. We caught females at infrequent intervals during the round-up in an attempt to sample a stratified (females > 3 years old) random portion of the population. We purposefully collared 9 bison females already being monitored by CSP for a social status study, which resulted in one dam/offspring pair both receiving radiocollars. We do not believe this violated the assumption of independence of locations as the dam's offspring underwent forced-weaning the fall after its birth, and forcibly-weaned bison calves typically do not re-associate with dams (Brookshier 2000). We determined the age of females by brand number because all bison in CSP are branded with their year of birth (e.g., 9 = 1999, 0 = 2000, 1 = 2001) during their first roundup as calves. We released all females into a fenced pasture for approximately 48 hours after capture to ensure calves that were separated during the roundup were re-united with their mothers. After 48 hours, we released the herd into CSP. We collared 1 female during the October 2007 roundup to replace an animal that died.

We captured 10 mature male bison and tagged each with mortality sensing ear-tag radio-transmitters (Advanced Telemetry Systems, Isanti, MN, USA) during fall 2006 (n = 1) and fall 2007 (n = 9). We selected males between the ages of 4 and 8 years for capture. We attempted to stratify the sample with a variety of ages, but did not capture male > 8 years old (with one exception; a 15-year old male was captured and tagged) to ensure members of our sample would not be harvested because CSP annually harvests most of the available 10-year old males during a trophy hunt. We determined ages of males by brand. We located male groups while driving throughout CSP on paved, gravel and two-track roads (Figure 1). Mature male groups do not typically associate with the large female/calf groups (Berger and Cunningham 1994, Mooring et al. 2005). We captured most of the males in meadows in forested areas along two-track roads. We attempted to tag males in different groups in different geographical areas of CSP. Males were sedated with a 7 ml of Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, IA, USA) reconstituted with 100 mg/ml xylazine hydrochloride and butorphanol. We antagonized this drug mixture with 1 cc of Antisedan® (Pfizer Animal Health, Exton, PA, USA), delivered intravenously. We monitored sedated males until they were resting sternally or standing upright.

Ear-tag transmitters had a life of approximately 9 months and were equipped with mortality sensors. We selected the fall season to place transmitters on bison males so that we could observe resource use outside of the breeding season. Bison typically breed during the mid-late summer in CSP (G. Brundige, Custer State Park, personal communication). We did not attempt to focus on breeding season use by males because males are with female groups during this time and information on female herd use was already obtained from the radio-collared females. In addition, we wanted to prevent damage to ear-tag transmitters that would be caused by fights among males during the breeding season.

We located female bison approximately 5 times per week, based on a rotating schedule, October 2005 – August 2008. We separated locations by 25–30 hour intervals. We attempted to locate male bison 5 times per week using the same collection periods, January 2006–December 2007. We visually confirmed locations or used triangulation techniques during night sampling periods or when weather conditions did not permit off-road travel. We visually confirmed 75.3% of female bison and 66.5% of male bison locations. Universal Transverse Mercator (UTM) coordinates of collared animals were recorded with a handheld GPS. When using triangulation, we only used azimuths < 20 min apart and obtain at least 2 azimuths > 45° apart. Telemetry accuracy was evaluated by Millspaugh et al. (2000) for CSP, and mean distance from estimated to true location was 176.1 m (range = 13.4–746.6 m) although this assessment included forested areas not frequented by bison and is likely a conservative estimate for our data. We used the computer program Location Of A Signal (LOAS; version 4.0, Ecological Software Solutions 2007) to estimate animal locations from two or more azimuths.

We monitored 50 pronghorn (26 males [M], 24 females [F]) with 30 transmitters, which included replacement of collars from mortalities, from November 2005–August 2008. We used a handheld netgun to capture pronghorn from a vehicle along roads throughout the prairie region of CSP (Figure 1). Pronghorn typically reside in open grasslands that allowed us to locate groups of pronghorn from a distance. We were able to approach to within 6 m of pronghorn on roads in CSP because this population was accustomed to a high level of vehicular disturbance. We also drove off-road to capture pronghorn, although the paved, gravel and two-track roads covered much of pronghorn territory in CSP (Figure 1). Each netted pronghorn was manually restrained, fitted with a mortality sensing radio-collar (Advanced Telemetry Systems, Isanti, MN, USA), aged according to incisor irruption and tooth wear (Dow and Wright 1962), and released. We attempted to maintain an equal distribution of collars among both sexes by selecting animals to tag during each capture based on the sex of pronghorn mortalities the previous season. We located pronghorn approximately 5 times per week, based on the same rotating schedule used above for bison locations, October 2005 – August 2008. We used the same techniques detailed above for bison to locate pronghorn. We were able to visually confirm 62.0% of pronghorn locations.

Data analysis

We used a two-step process to analyze spatial overlap among ungulate species in CSP. First, we developed a classification tree to identify areas on the landscape where habitat use among species was similar and calculated an index of overlap. Second, we used this overlap index as the response variable in a general linear model to rank hypotheses regarding the relationship between the overlap index and habitat attributes. The first step was important in identifying where on the landscape overlap among all 5 ungulate species was likely to occur, and the second step allowed us to identify the primary mechanisms affecting spatial heterogeneity in overlap.

An important assumption in our analysis was that ungulates were using resources in the same manner across the years of our data sets, and that populations of ungulates would not fluctuate to an extent that would change the habitat use of another ungulate. We are comfortable with this assumption because most ungulate populations, with the exception of elk, were relatively stable, and because features in the landscape did not change substantially over the time period that encompassed our location data (G. Brundige, Custer State Park, personal communication). Elk populations decreased from a mean of 903 elk (95% CI = 787–1021) during 1993–1997, the time period that elk locations were recorded, to a mean of 553 elk (95% CI = 426–681) during 2005–2008, the time period that bison and pronghorn locations were recorded. We do not believe that the decrease in elk numbers would have significantly changed resource selection of the ungulate community 2005–2008, since average densities only changed from 0.0003 elk/km^2 for 1993–1997 to 0.0002 elk/ km^2 2005–2008. We excluded 136 bison and 107 pronghorn locations that occurred in forested units where timber harvest or wildfire occurred after 2002, the time period that our GIS vegetation layers were developed.

Identifying areas of habitat overlap. Classification trees are used to predict membership of classes (i.e., ungulate species) of a categorical dependent variable from measurements on one or more predictor variables (i.e., habitat attributes). The tree is built through binary recursive partitioning, an iterative process of splitting the data into partitions. We used a classification tree to classify habitat use by bison, white-tailed deer, mule deer, pronghorn and elk. We used the locations of each species as the categorical dependent variable in the classification tree, and used 20 habitat attributes as predictor variables (Table 1). These habitat attributes were determined for each location in GIS.

To build the classification tree, we combined habitat attribute data at each species location and imported the information into CART® v6.0 (Salford Systems 2008) for further analysis. We used the Gini algorithm as a splitting rule, which is the default splitting rule in CART and performs well with most data sets (Steinberg and Golovnya 2006). We ran four separate models for each season [Spring (1 March – 31 May), Summer (1 June – 31 August), fall (1 September – 31 November), and winter (1 December – 29 February)]. The fall season CART analysis did not contain any locations of mule deer or white-tailed deer because Woeck (2003) did not record locations during this season. We corrected for the effect of different sample sizes of species locations by computing classification probabilities relative to the sample size of each species to ensure larger classes (bison, pronghorn and elk) are not given more weight in the analysis than smaller classes (white-tailed deer and mule deer; Steinberg and Golovnya 2006). We used the smallest classification tree within 1 SE of the best tree based on cost complexity analysis to evaluate habitat overlap among the 5 species. Cost complexity analysis is a process that chooses the smallest tree which maximizes prediction accuracy (Steinberg and Golovnya 2006).

We used 10-fold cross validation to evaluate the predictive accuracy of the final tree for each season (Steinberg and Golovnya 2006). Predictive ability of the classification tree should be inverse to the amount of habitat overlap among the ungulate assemblage, because a model that performed poorly in separating the habitat attributes used among the species would correspond to a high degree of habitat overlap. We thus used the predictive ability of the classification tree to gauge the amount of habitat overlap occurring among the seasons.

Measures of overlap. We exported the final trees, which contained the number of locations per species in each end node. For each classification end node (the endpoint of the tree that contains the classification prediction) of the final tree, we computed the within-node predictive probability for each species. This probability was an extension of Bayesian theorem and is calculated:

$$P(B|A) = \frac{P(A|B) \cdot P(B)}{P(A)}.$$

Using this theorem, the conditional property of *B* given *A* can be expressed in terms of the conditional probability of *A* given *B*. One application of Bayes theorem leads to Bayesian analysis where *A* denotes the parameters to be estimated ($\underset{\sim}{\theta}$), and *B* denotes the data $\underset{\sim}{x}$, as

$$P(\underset{\sim}{\theta}|\underset{\sim}{x}) = \frac{P(\underset{\sim}{x}|\underset{\sim}{\theta}) \cdot P(\underset{\sim}{\theta})}{P(\underset{\sim}{x})}.$$

The $P(\underset{\sim}{\theta}|\underset{\sim}{x})$ portion of the equation is the Bayes' posterior distribution expressed in terms of the likelihood function (i.e., $P(\underset{\sim}{x}|\underset{\sim}{\theta})$), the prior distribution for the parameters $P(\underset{\sim}{\theta})$ and the marginal distribution for the data $P(\underset{\sim}{x})$. The marginal distribution for the data $P \;\underset{\sim}{x}$ can be found by integrating the joint probability $P \;\underset{\sim}{x} \cap \underset{\sim}{\theta}$ over values of $\underset{\sim}{\theta}$, where

$$P \;\underset{\sim}{x} = \sum^{\underset{\sim}{\theta}} P \;\underset{\sim}{x} \cap \underset{\sim}{\theta} = \sum^{\underset{\sim}{\theta}} P \;\underset{\sim}{x} \,\middle|\, \underset{\sim}{\theta} \cdot P \;\underset{\sim}{\theta} \;.$$

Combining these equations leads to the Bayes' posterior theorem, which is:

$$P(C_j \mid N_i) = \frac{p_j \times \dfrac{n_{ji}}{N_j}}{\sum\limits_{n=i} \left[p_j \times \dfrac{n_{ji}}{N_j} \right]}$$

where $P(C_j|N_i)$ = the predictive probability for each class (or species; C_j) within an endnode (N_i) and p_j = the prior probability for species *j*, n_{ji} = the number of locations of species *j* in node *i*, N_j = the total number of locations of species *j* (M. Golovnya, Salford Systems, personal communication). For our analyses we assumed the prior probabilities were equal for all species and were thus = 1. We summed the squared within-node predictive probabilities for all species for each end node and subtracted that value from 1 for the overlap score:

$$Overlap = \left(1 - \sum \left[P(C_j \mid N_i)\right]^2\right).$$

This final overlap score thus accounts for the misclassification rate of the node; a high misclassification rate would correspond to areas where overlap would presumably occur. This is a novel approach in that we are relying on the lack of fit of the classification tree to indicate overlap. This overlap value ranges from 0, when only 1 species was associated with an endnode, to 0.83 when all 6 species had equal predictive probabilities for an endnode. We calculated this overlap score for each endnode in each seasonal classification tree.

Spatially explicit overlap. We used the final trees to develop raster queries in ArcGIS 9.2 (Environmental Systems Research Institute 2006) to display the spatial area that corresponded to each end node in the classification tree. Each raster query produced *n* pixels (30 m^2 resolution) which were given the same overlap score as the endnode used to produce them. These maps were used to identify potential 'hotspots' of species overlap in CSP. We produced overlap maps for each season.

Hypothesis testing. Because CART has no ability to identify which variables are associated with heterogeneity within nodes, we used a separate analysis to test hypotheses about the relationship between the overlap index and environmental attributes. We used the index value created from the CART analysis as the response variable in a general linear model to assess what resources influence habitat overlap of ungulates. We used the index value grid, with 240 m cells, and used Hawth's tools (Beyer 2004) to associate grid nodes with resource attributes. Next, we used the 'ruf.fit' package (Marzluff et al. 2004; available at www.csde.washington.edu/~handcock/ruf/) in R (R Development Core Team 2006) to fit *a priori* models (listed below) for habitat overlap among the ungulate assemblage. The 'ruf.fit' package accounted for the spatial autocorrelation among grid cells using a Matern function of the Euclidian distance between two grid points, with the range determined by the rate of decrease in correlation between estimates of overlap with distance (Marzluff et al. 2004). We hypothesized that nonlinear relationships were plausible between many of the variables and the overlap index. Therefore, we first evaluated psuedothreshold and quadratic forms for every variable in a univariate model (using the GLM statement in R), and used the form of the function with the lowest Akaike information criterion (AIC) in all models.

Hypotheses. We evaluated 7 main hypotheses to explain seasonal overlap, each associated with one of the important underlying factors: forage, water, predator avoidance, thermal cover, predictable human-related disturbance, unpredictable human-related disturbance, and spatial niche separation (Table 2). These hypotheses were based on the available literature regarding habitat use and habitat overlap among ungulate species. Models were developed to represent each hypothesis. When more than one model was needed to represent the main hypothesis, we included separate sub-hypotheses. The alternative models corresponding to each hypothesis are described below. We used an information-theoretic approach (Burnham and Anderson 1998) to determine the relative importance of each hypothesis as it relates to seasonal habitat overlap. We ranked hypotheses according to the Akaike Information Criterion (AIC) for each model for each season (Burnham and Anderson 1998).

Forage Hypothesis. All ungulates rely on a diet of plant species, so the hypothesis that habitat overlap would be associated with palatable forage biomass is intuitive and has support in the literature (Fryxell 1995). We developed 3-4 different subhypotheses to represent the overall forage hypothesis. For the simplest representation of forage we used estimates of forage biomass from a model developed by Keller (Chapter 1). This forage biomass model includes parameters for range and woodland grazable site, slope, elevation, canopy cover, whether the site was in a prairie dog colony, current annual spring precipitation, previous year spring precipitation, and ordinal date of last spring frost. We used the 25-year mean (1983-2008) for spring precipitation variables and the mean ordinal date of last spring frost for 2004-2008. Palatable forage production was estimated by multiplying total biomass by proportion of production that was considered palatable to any CSP ungulate species based on Larson and Johnson (1999). Additionally, because each ungulate species has its own unique dietary niche, we separated palatable forbs, grasses, and shrubs as a sub-hypothesis. We also used the palatable forage biomass with information on palatable species diversity to develop a biomass diversity hypothesis. To measure diversity we used the Shannon's diversity index (Krebs 1989) to calculate a diversity score for each range and woodland grazable site in CSP. We multiplied this diversity score by the total palatable biomass to create a 'diversity-adjusted' biomass value. High values represent areas of both high palatable biomass and high diversity.

Water Hypothesis. Water can be important components of ungulate resource selection (Mackie 1970, Senft et al. 1987, Johnson et al. 2000, Stewart et al. 2002) thus we hypothesized ungulate species may co-occur at water features in CSP. Models representing the water hypothesis included 3 variables, distance from flowing stream, distance from pond, and distance from intermittent stream. We separated these features because topography, hiding cover, and water availability may differ among these water types. Each variable represented the Euclidian distance from each feature, as calculated using the Spatial Analyst toolbar (Environmental Systems Research Institute 2006) in ArcGIS 9.2. Coverage of water features were obtained from a vegetation classification map developed by Cogan et al. (2004), which used stereo-aerial photography to classify features in CSP based on the National Vegetation Classification System.

Predator Avoidance. Although predator avoidance strategies vary among the ungulate species (Geist 1998) present at CSP, as well as the predator they are avoiding (Geist 1998), there may be certain landscape features that facilitate predator avoidance for all species. Two factors that were relevant to the majority of the ungulate assemblage are hiding cover and predator presence. Hiding cover may be important for ungulate species that rely on hiding strategies for predator avoidance, especially for females seeking cover for fawns or calves. Forest density and strata type affect the ability of a predator to detect ungulates. Our hiding cover hypothesis consisted of 4 variables, a multi-strata forest categorical variable (0,1), a single-strata forest categorical variable (0,1), number of trees per acre, and distance to forest edge. We included a distance to forest variable in our predator avoidance hypothesis because mountain lions are most often seen in the forested regions of CSP (G. Brundige, Custer State Park, personal communication). Mountain lions have the ability to depredate all of the ungulates in CSP, with the exception of adult bison. Single- and multi-strata forest height data were obtained from the Cogan et al. (2004) vegetation classification layer. Data on trees per acre were obtained from available CSP forest inventory data. Distance to forest was calculated using forest polygons derived from the Cogan et al. (2004) vegetation coverage database.

Thermal cover. Thermal cover was represented by 3 separate sub-hypotheses. The forest height subhypothesis consisted of a multi-strata forest categorical variable, a single-strata forest categorical variable, canopy cover, and trees per acre. Forest height and trees per acre variables are described above. We obtained canopy cover data from the National Land Cover Database (Homer et al. 2004). The tree size subhypothesis consisted of indicator variables denoting 5 tree size categories (none, sapling [< 6” dbh], medium [6-12” dbh], large [12-16” dbh], and very large [>16” dbh]), which were obtained from the Cogan et al. (2004) vegetation database, and canopy cover and trees per acre. The topographical subhypothesis consisted of a radiation and heat load variable. Radiation was calculated from the digital elevation model (DEM) using the Area Solar Radiation tool in Spatial Analyst toolbox (Environmental Systems Research Institute 2006). This tool uses variation in elevation, slope, aspect, shadows cast by topographic features, and variation in day and time of year to calculate insolation. We computed solar radiation separately for each season to account for differences due to daylength. Heat load is based on aspect and is calculated with the following equation: $\frac{1-\cos(\theta-45)}{2}$, where θ = aspect in degrees east of north (McCune and Keone 2002). This index results in rescaling aspect to a scale of 0 to 1, with 0 being the coolest slope (northeast) and 1 being the warmest slope (southwest).

Human-related disturbance. Approximately 1.6 million people visit CSP in a typical year (C. Pugsley, Custer State Park, personal communication) so it is likely that public visitation is the major source of disturbance in CSP. Therefore we modeled disturbances using features related to human visitation, such as roads and campgrounds. Habituation of wildlife to certain predictable disturbances is well-documented (Bejeder et al. 2006, Baudainis and Lloyd 2007, Haskell and Ballard 2008). Thus, we hypothesized ungulates would react differently to disturbances they may expect to encounter in certain areas of CSP, and separated our disturbance hypothesis into predictable and unpredictable subhypotheses. Because public visitation of the park is highly seasonally dependent, ungulates may have become less habituated to use of certain road types during different seasons. Paved, gravel and two-track roads all occur in CSP (Figure 1). Paved roads were highly traveled during all seasons as two of the three paved roads are federal or state highways, and the other is the Wildlife Loop road. Thus, we classified these areas, along with areas of human activity (e.g., buildings and campgrounds) as having predictable disturbance for every season. We assumed trails and two-track roads that were used by park personnel acted as areas of unpredictable disturbance during all seasons. However, we hypothesized that the predictability of disturbance on gravel roads varied with season, where the higher occurrence of tourists during spring and summer resulted in more predictable disturbance as compared to fall and winter where gravel roads acted as areas of unpredictable disturbance. We computed relative densities of disturbance features to characterize their presence throughout the park, using the line density tool in Spatial Analyst. Because density did not account for topographical or vegetative buffering from roads, we included a "visibility" metric in an alternative submodel to both predictable and unpredictable hypotheses. This visibility metric measured the probability that an animal could be viewed from the road based on topographical features and vegetation structure (G. Roloff, University of Michigan, personal communication).

Spaial niche separation. We hypothesized that overlap would occur at high-quality resources at the edges of habitat patches if spatial niche separation were occurring. We classified a 'patch' as one of 11 distinct habitat types (Figure 2) based on Cogan et al. (2004), and extracted the edges of the polygons of each habitat type. Patch edge density was calculated with the Density tool (Environmental Systems Research Institute 2006) in ArcGIS 9.2, and is expressed as km of patch edge per km^2 (Figure 2). We identified three main resources to represent high quality resources in 3 separate submodels: forage biomass and diversity, water density, and intermittent streams. Each resource was used in a model with patch edge density and included an interaction between patch edge density and the resource.

Model validation. We used *k*-fold cross validation (Kohavi 1995) to evaluate our top-ranked seasonal overlap models. We divided our data into 3 subsets, each containing training and testing groups. We used Huberty's (1994) rule-of-thumb to compute a training-to-testing ratio of 0.8:0.2. We used random sampling to select data for placement in the testing group. For each fold of the cross-validation, we used the training dataset to estimate model parameters, and compared predicted values to the observed values in the testing dataset. We calculated the mean bias error (MBE) and root mean square error (RMSE) between the observed and predicted values for each fold in the cross-validation. Mean bias error is an index of the magnitude of the under- or over-prediction of the model and is calculated as

$$MBE = \frac{\sum_{i=1}^{n} (p_i - o_i)}{n}$$

where p_i is the *i*th predicted value, o_i is the *i*th observed value, and *n* is the number of data pairs. The RMSE is an index of the average deviation between predicted and observed pairs regardless of sign, and is calculated as

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} (p_i - o_i)^2}{n}}.$$

We averaged MBE and RMSE values across folds for each seasonal model.

RESULTS

Seasonal habitat overlap

Habitat overlap was seasonally dynamic, and while we observed consistent patterns of overlap among some species pairs, seasonal changes in overlap among species pairs were also apparent. Sample sizes were large for most ungulate species per season, with the exception of the lack of mule deer and white-tailed deer location during the fall. We used 1829–2685 female bison locations, 68–458 male bison locations, 2225–3034 elk locations, and 1709–2697 pronghorn locations to build each seasonal CART model. We used 439–1134 and 512–1299 mule and white-tailed deer locations, respectively, to build the winter, spring and summer CART models. Habitat overlap among ungulate species was greatest in the winter, moderate in fall and spring, and lowest during the summer (Table 3). During all seasons, male bison use was most accurately predicted compared to all other species (Tables 4–8), suggesting male bison use the most unique habitat attributes among the ungulate assemblage. Pronghorn use was the least accurately predicted each season, except for winter, when elk locations were the least accurately predicted (Tables 4–8), suggesting pronghorn (during spring, summer and fall) and elk (during winter) are least distinct in habitat use among the ungulate assemblage. The high amount of habitat overlap that occurred among pronghorn and female bison likely contributed to the difficulty in accurately predicting habitat use as “uniquely pronghorn”; between 22 and 48% of pronghorn locations were incorrectly predicted as bison use each season (Tables 4–8). Elk and male bison used similar habitats during the fall and winter, when 14.3 and 11.7%, respectively, of elk locations were incorrectly predicted as male bison (Tables 6 and 7), but not during the spring and summer, when misclassification rates were 5.3 and 3.6%, respectively (Tables 4 and 5). Elk also appeared to overlap moderately with bison female (misclassification rate of 2.7–10.8%) and white-tailed deer (misclassification rate of 5.9–12.4%) in habitat use (Tables 4–8). White-tailed deer and mule deer, had moderate amounts of overlap (misclassification rate of 4.7–10.1%), which was highest during the spring and lowest during the winter (Tables 4–8).

Comparison of hypotheses explaining heterogeneity in overlap

The spatial niche hypothesis received the most support during all seasons except summer. There was little uncertainty in model rankings; no other model received > 0.05% of the weight for fall, winter or spring. During fall and winter, the patch edge density model with forage biomass and diversity was the most supported model (Table 9). Habitat overlap was greatest in areas of high patch edge density with high forage biomass and diversity during fall (Figures 3 and 4). During winter, overlap was positively associated with areas of high forage biomass ($\geq$ 2000 kg ha^{-1}) and high patch edge density (Figures 5 and 6). At areas of low biomass (< 1000 kg ha^{-1}) overlap was negatively associated with patch edges (Figure 6). Conversely, during fall, overlap was positively associated with patch edges at any amount of biomass > 0 kg ha^{-1} (Figure 4). During spring, the patch edge density model with distance to intermittent streams received the most support (Table 9). Habitat overlap was positively related to patch edge density, and was highest close to intermittent streams (Figures 7 and 8). During summer, the water hypothesis was most supported (Table 9), with little model uncertainty. Overlap was highest away from ponds and streams, and close to intermittent streams (Table 9). Distance to intermittent streams was the most influential parameter on habitat overlap (Figures 9 and 10).

All models passed goodness-of-fit tests against the null, or intercept only, models (all *P*s $\leq$ 0.0001). The MBE for the seasonal models based on the cross validation was very low across seasons (Table 10), which means the magnitude of the average over- or under-prediction by the model was small. The RMSE, the average deviation between the observed and predicted values regardless of sign, was larger and varied from between 39 to 48% of the mean overlap score for each season (Table 10). This RMSE is indicative of a model that performs marginally well, as all 95% confidence intervals using the mean overlap score and substituting the RMSE for the standard error were wide, but did not encompass 0.

DISCUSSION

Habitat overlap among CSP ungulates followed seasonal patterns typical of temperate ungulate assemblages; overlap was higher during the winter and lower during the summer (Schwartz and Ellis 1981, Jenkins and Wright 1988, Gordon and Illius 1989, Heroldova 1996). The pattern we observed coincides with the quality and availability of forage in the Northern Great Plains; standing crop and forage quality are at the peak during the spring and summer (Heitschmidt et al. 1995). However, Wydeven and Dahlgren (1985) observed the opposite seasonal relationship of habitat overlap among bison, elk, pronghorn and mule deer in Wind Cave National Park; and found overlap was highest during summer and lowest during winter. The differences between our results and those of Wydeven and Dahlgren (1985) may be due to methodology, temporal change, or differences between the two study areas. The Wydeven and Dahlgren study used census techniques to estimate habitat use of ungulates which likely missed some aspects of ungulate resource selection, in a less diverse habitat, and under different densities of bison, elk, and prairie dogs (Wydeven and Dahlgren 1985). Using different methods, Woeck (2003) also found that habitat overlap among elk, mule deer and white-tailed deer in CSP was greatest during the winter and lowest during the summer. Higher habitat overlap during periods of low resource quality has also been observed among ungulates in northern Montana (Jenkins and Wright 1988), western India (Bagchi et al. 2003), and New Forest in southern England (Putnam 1996). Given the diminishing amount of forage quantity and quality as summer transitioned to winter, ungulates in CSP likely experienced greater habitat overlap as they expanded ranges in search of food and as the diversity of the forage available decreased.

The significance of habitat patch edges to habitat overlap during most seasons in CSP could be indicative of coevolutionary divergence or competition. Spatial niche divergence and resource partitioning has also been observed in ungulate assemblages in Wind Cave National Park adjacent to CSP (Wydeven 1979), the western United States (Singer 1979, Singer and Norland 1994, Johnson et al. 2000, Stewart et al. 2002, Coe et al. 2005), and in numerous other regions globally (Putnam 1996, Bagchi et al. 2003, Estes et al. 2006, Henley et al. 2007). Resource partitioning is often interpreted as a lack of competition, however, as Putnam (1996) asserts, ecological separation itself may be an explicit response to competition. However, habitat edges are often areas of high plant species richness (Brothers and Spingarn 1993, Fraver 1994). Therefore, habitat niche edges could actually be areas of attraction to resources at these edges rather than default areas of interaction at patch boundaries. However, forage diversity alone was not important without habitat patch edges to account for heterogeneity in overlap within CSP, suggesting the patch edge itself, not just forage diversity associated with the edge, was important.

Although it was clear that water was the most important mechanism regulating habitat overlap during the summer, the relationship between specific water sources and overlap was unexpected. Ungulates overlapped at areas far from ponds and streams, rather than near the features as we expected. Perhaps it should not be surprising that the entire ungulate assemblage did not overlap at water sources. Although water has been documented as an important feature in mule deer (Mackie 1970, Stewart et al. 2002) and elk (Mackie 1970, Stewart et al. 2002) habitat selection, ungulates in Kruger National Park in Africa varied in their association with water sources (Gaylord et al. 2003, Smit and Grant 2009), and water sources were not important to bison habitat selection in Utah (Van Vuren 2001). However, these results do not necessarily suggest that water is unimportant to the ungulate assemblage. Ungulates in CSP are never > 7.1 km from a flowing stream and never > 4.0 km from a pond, thus fresh-water sources may not be a limiting resource considering all ungulates in CSP certainly have the ability to reach a water source within a 24-hour period. Moreover, if the actual time spent at water sources was low, our sampling scheme may have been unlikely to capture animal locations at water. Van Vuren (2001) found that bison spent an average of 21 minutes at water sources in Utah, and Rosenstock et al. (2004) found that mule deer spent an average of 5 minutes at artificial water sites in southern Arizona.

There are also several explanations for ungulate avoidance of water sources. Water sources may be areas of high predator density (Rosenstock et al. 1999), and broken terrain and high forage biomass associated with some streams and ponds could provide excellent hiding cover for predators such as mountain lions and coyotes. Schmidt and DeStefano (1996) found an increase in predator tracks and sign associated with artificial water sources in Arizona, and African lions have shown associations with standing water in Kruger National Park (Gaylord et al. 2003). We found that pronghorn in CSP avoided streams, but occurred near ponds (Chapter 2). Furthermore, as summer progresses, erosion and foraging from the large herd of bison and other ungulates can lead to bare ground surrounding many of the ponds throughout the prairie region of CSP. Thus, ungulates would need to move further away from water sources to forage. Similarly, Gaylord et al. (2003) found that some large grazers in Kruger National Park spent more time away from water due to poor foraging conditions associated with water sources.

In contrast, intermittent streams appear to be an important feature for CSP ungulates during the spring and summer. Intermittent streams in CSP rarely hold water expect during the spring. However, they tend to be wetter than surrounding areas and support more hardwoods and lush vegetation. These drainages may provide important forage for elk, deer and pronghorn and protection from the summer heat. Many of these forested drainages occur where the rugged Black Hills meet the Black Hills footslopes on the edge of the prairie, and may be the closest forest cover for bison seeking cover during the day. Although intermittent water sources are not often included as unique resources in habitat selection studies, Stewart et al. (2002) is an exception. Stewart et al. (2002) found that intermittent water sources were more important than permanent water sources in elk habitat selection models in the Starkey Experimental Forest, in Oregon, while both permanent and intermittent water sources were important to mule deer and cattle. Our results suggest the intermittent drainages may be more important to resource use by > 1 ungulate species than previously thought.

We found no evidence to suggest thermal cover, hiding cover, disturbance, or forage biomass were important to habitat overlap among the entire ungulate assemblage. Given that the thermal cover hypothesis has consistently failed to exhibit empirical support in the literature despite the support it once held as an *a priori* belief (Cook et al. 1998 and 2004), and that not all ungulates in the assemblage rely on hiding cover as a predator avoidance strategy (Berger and Cunningham 1994, Byers 1997, Geist 1998), the failure of these two hypotheses to explain heterogeneity in overlap is not surprising. We were surprised that disturbance, given the high level of human-related disturbance occurring in CSP, and that forage, given that it is generally considered the most important feature driving ungulate resource selection, were not important. However, analyses of species-specific resource selection of pronghorn and bison in CSP have shown that these ungulates in CSP do not avoid areas of high predictable disturbance, or that they only avoid those areas during the periods of highest use. Woeck (2003) found that white-tailed deer and mule deer varied in their association with roads based on the season, although elk have shown to be sensitive to roads in the Park (Millspaugh 1999). The response of the assemblage to disturbance in CSP appears to vary, thus they do not overlap in areas that are far from those disturbances. As for the forage hypothesis, given the diversity of diets in the ungulate population in CSP, simple biomass estimates may not be enough to accommodate areas where the total ungulate assemblage would overlap in habitat use without measures of species diversity. Ungulate species are likely not selecting habitats solely based on biomass, but on biomass amounts in association with other seasonal stressors, such as water, as analyses of bison and pronghorn resource selection have shown (Chapters 2 and 3).

Although patch edges and intermittent streams were important to explain overlap among the entire ungulate assemblage, undoubtedly overlap took place between smaller numbers of ungulate species elsewhere in CSP. For example, female bison and pronghorn locations were most often misclassified as one another, implying similar habitat use during all seasons, likely because both species evolved to utilize broad, open plains. Thus, overlap between these two species was likely occurring elsewhere than habitat patch edges. High habitat overlap between bison and pronghorn has been reported elsewhere where the two species co-exist (Wydeven 1979, Singer and Norland 1994). However, diet overlap between these two species is low in CSP (Chapter 4), and other areas (Wydeven 1979, WICA; Singer and Norland 1994, Yellowstone National Park), and the different digestive physiology of the two species (Putnam 1988) suggests the potential for competition between bison and pronghorn is minimal.

Based on habitat and diet overlap (Chapter 4) of CSP ungulates, potential for competition among ungulates in CSP may be greatest between bison males and elk, and white-tailed deer and elk. Elk are often described as habitat and diet generalists, with the ability to exploit a much broader niche in the environment than other sympatric ungulates (Hudson et al. 1976, Jenkins and Wright 1988). Thus, that misclassification of locations occurs most frequently between elk and other species is not surprising. Moderate to high habitat overlap between bison and elk has been reported for Wind Cave National Park (Wydeven 1979), Yellowstone National Park (Singer and Norland 1994), and Elk Island National Park (Telfer and Cairns 1979). However, Singer and Norland (1994) found no evidence for interspecific competition between bison and elk despite large populations increases of both species from 1967–1988 in Yellowstone National Park. Similarly, Wydeven (1979) found low competitive potential between bison and elk based on diet in Wind Cave National Park. Because elk and white-tailed deer are only sympatric on a small portion of each species' range (Miller 2002) literature on potential competitive interactions is scarce. Jenkins and Wright (1988) found competitive potential to be high for white-tailed deer and elk in the northern Rocky Mountains, especially during winter. The competitive potential between the two species is described as low by Miller (2002), but that conclusion is based on data from populations in the northwestern United States and Canada. The potential for competition between elk and white-tailed deer may be greater in CSP than other areas given the high number of ungulate species and differences in forage species between the Black Hills and other reported studies.

MANAGEMENT IMPLICATIONS

Our work provides insight into mechanisms of habitat overlap in large herbivore assemblages. The results suggest the large herbivore assemblage in CSP maintain spatial niches, and overlap is greatest at patch edges with high quality resources. These may be important areas to monitor range condition because they are likely to be bellwethers of ecosystem health, and are likely the first areas to show degradation from overly-dense herbivore populations. Thus, we suggest managers in CSP focus monitoring activities at the prairie-forest ecotone and intermittent streams.

Although features such as hiding cover, standing water, or human disturbance were unimportant to explain overlap of the entire ungulate assemblage, these features may still be important to individual ungulate species. Indeed, human disturbance and water have been demonstrated to be important to bison, pronghorn and elk resource selection in CSP (Chapter 2, Chapter 3, Millspaugh 1999). However, due to the diversity of foraging and predator avoidance strategies of ungulates in CSP it was unlikely that one of these features would be most important to explain habitat overlap among the entire ungulate assemblage. An interesting future direction in research would be to examine mechanisms influencing habitat overlap among pairs of ungulate species, especially those that have similar foraging or predator avoidance strategies.

Our data are consistent with the hypothesis that coevolutionary divergence limits competition in large herbivore assemblages, but niche divergence itself does not rule out competition in the assemblage. In fact, the potential for competition still existed between certain pairs of species. Accurate monitoring of all components of the herbivore assemblage is important, especially closed preserves, to maintain healthy conditions for both the ungulate assemblage and the prairie ecosystem.

LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076–1088.

Avey, J. T., W. B. Ballard, M. C. Wallace, M. H. Humphrey, P. R. Krausman, F. Harwell, and E. B. Fish. 2003. Habitat relationships between sympatric mule deer and white-tailed deer in Texas. Southwest Naturalist 48:644-653.

Bagchi, S., S. P. Goyal, and K. Sankar. 2003. Niche relationships of an ungulate assemblage in a dry tropical forest. Journal of Mammalogy 84:981–988.

Barrett, R. H. 1982. Habitat preferences of feral hogs, deer, and cattle on a Sierra foothill range. Journal of Range Management 35:342–346.

Baudains, T. P., and P. Lloyd. 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Animal Conservation 10:400–407.

Ben-Shahar, R., and J. D. Skinner. 1988. Habitat preferences of African ungulates derived from uni- and multivariate analyses. Ecology 69:1479–1485.

Berger, J., and C. Cunningham. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York, New York, USA.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. http://www.spatialecology.com/htools.

Bejeder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: Use and misuse of habituation, sensitization and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395:177–185.

Brookshier, J. S., and W. S. Fairbanks. 2003. The nature and consequences of mother-daughter associations in naturally and forcibly weaned bison. Canadian Journal of Zoology 81:414–423.

Brothers, T. S., and A. Spingarn. 1993. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6:91–100.

Brunjes, K. J., W. B. Ballard, M. H. Humphrey, F. Harwell, N. E. McIntyre, P. R. Krausman, and M. C. Wallace. 2009. Home-range size and overlap of sympatric male mule and white-tailed deer in Texas. Western North American Naturalist 69:125–130.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multi-model inference. Springer-Verlag, New York, New York, USA.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. The University of Chicago Press, Chicago, Illinois, USA.

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences 71:3073–3077.

Chapman, N. G., K. Claydon, M. Claydon, P. G. Fordie, and S. Harris. 1993. Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behavior, social organization and activity. Journal of Zoology 229:623–640.

Clover, M. R. 1954. Single-gate deer trap. California Fish and Game 42:199–201.

CSP. 1995. Custer State Park resource management plan 1995–2010. Unpublished document.

Cobb, M. A., P. J. Gogan, K. D. Kozie, E. M. Olexa, R. L. Lawrence, and W. T. Route. 2004. Relative spatial distributions and habitat use patterns of sympatric moose and white-tailed deer in Voyageurs National Park, Minnesota. Alces 40:169–191.

Coe, P. K., B. K. Johnson, K. M. Stewart, and J. G. Kie. 2005. Spatial and Temporal Interactions of Elk, Mule Deer, and Cattle. Pages 150-158 *in* M. J. Wisdom, editor. The Starkey project: a synthesis of long-term studies of elk and mule deer. Reprinted from the 2004 Transactions of the North American Wildlife and

Natural Resources Conference, Alliance Communications Group, Lawrence, Kansas, USA.

Cogan, D., H. Marriott, and M. Pucherelli. 2004. Custer State Park, South Dakota, vegetation mapping project. Technical Memorandum 8260-04-01. U. S. Bureau of Reclamation Technical Service Center, Remote Sensing and GIS Group, Denver, Colorado, USA.

Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1998. Influence of forest cover on condition of elk in summer and winter. Wildlife Monographs 141:1–61.

Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 2004. Thermal cover needs of large ungulates: a review of hypothesis tests. Transactions of the North American Wildlife and Natural Resources Conference 69:708–726.

Dix, R. L. 1958. Some slope-plant relationships in the grasslands of the Little Missouri Badlands of North Dakota. Journal of Range Management 11:88–92.

Dodge, W. E., and A. J. Steiner. 1986. XYLOG: a computer program for field processing locations of radio-tagged wildlife. U. S. Department of the Interior, Fish and Wildlife Service Technical Report 4, Washington D.C., USA.

Dow, S. A., and P. L. Wright. 1962. Changes in madibular dentition associated with age in pronghorn antelope. Journal of Wildlife Management 26:1–18.

Dublin, H. T., A. R. Sinclair, S. Boutin, E. Anderson, M. Jago, and P. Arcese. 1990. Does competition regulate ungulate populations? Further evidence from the Serengeti, Tanzania. Oecologia 82:283–288.

Ecological Software Solutions, 2007. LOAS Version 4.0. [software] Ecological Software Solutions, Sacramento, CA, USA.

Environmental Systems Research Institute. 2006. ArcGIS: Release 9.2 [software] Redlands, California: Environmental Systems Research Institute, 1999–2006.

Estes, R. D., J. L. Atwood, and A. B. Estes. 2006. Downward trends in Ngorongoro Crater ungulate populations 1986–2005: conservation concerns and the need for ecological research. Biological Conservation 131:106–120.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke river basin, North Carolina. Conservation Biology 8:822–832.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1): 11. [online] URL: http://www.consecol.org/vol6/iss1/art11

Fryxell, J. M. 1995. Aggregation and migration by grazing ungulates in relation to resources and predators. Pages 257–273 *in* A. R. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. The University of Chicago Press, Chicago, Illinois, USA.

Gaylord, A., N. Owen-Smith, and J. Redfern. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. Pages 171–188 *in* J. T. du Toit, H. C. Biggs, and K. H. Rogers, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, Washington, D. C., USA.

Geist, V. 1998. Deer of the World: their evolution, behavior and ecology. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Gordon, I. J., and A. W. Illius. 1989. Resource partitioning by ungulates on the Isle of Rhum. Oecologia 79:383–389.

Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. The American Naturalist 155:435–453.

Hanley, T. A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. Journal of Applied Ecology 21:423–436.

Haskill, S. P., and W. B. Ballard. 2008. Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. Canadian Journal of Zoology 86:627–637.

Henley, S. R., D. Ward, and I. Schmidt. 2007. Habitat selection by two desert-adapted ungulates. Journal of Arid Environments 70:39–48.

Heroldova, M. 1996. Dietary overlap of three ungulate species in the Palava Biosphere Reserve. Forest Ecology and Management 88:139–142.

Heitschmidt, R. K., E. E. Grings, M. R. Haferkamp, and M. G. Karl. 2995. Herbage dynamics on 2 northern Great Plains range sites. Journal of Range Management 48:211–217.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Devlopment of a 2001 national land cover database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Huberty, C. J. 1994. Applied discriminant analysis. Wiley Interscience, New York, New York, USA.

Hudson, R. J., D. M. Hebert, and V. C. Brink. 1976. Occupational patterns of wildlife on a major east Kootenay winter-spring range. Journal of Range Management 29:38–43.

Ilse, L. M., and E. C. Hellgren. 1995. Spatial use and group dynamics of sympatric collared peccaries and feral hogs in southern Texas. Journal of Mammalogy 76:993–1002.

Jenkins, K. J., and R. G. Wright. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. Journal of Applied Ecology 25:11–24.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.

Keuroghlian, A., D. P. Eaton, and W. S. Longland. 2004. Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biological Conservation 120:411–425.

Kohavi, R. 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection. Pages 1137–1143 *in* Proceedings of the 14th International Joint Conference on Artificial Intelligence. Montreal, Canada.

Krebs, C. 1989. Ecological methodology. HaperCollins, New York City, New York, USA.

Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota State University, College of Agriculture and Biological

Sciences, South Dakota Agricultural Experiment Station, Brookings, South Dakota, USA.

Latham, J., B. W. Staines, and M. L. Gorman. 1997. Correlations of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer densities in Scottish forests with environmental variables. Journal of Zoology 242:681–704.

Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. Ecology 83:2037–2048.

Lynch, B. R., and R. Rochette. 2009. Spatial overlap between sub-adult American lobsters, *Homarus americanus*, and the invasive European green crab *Carcinus maenas*. Journal of Experimental Marine Biology and Ecology 369:127-135.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildlife Monographs 20:1–79.

Maichek, E. J., K. L. Schuler, and M. E. Payton. 2004. Daily and seasonal behavior of bison on an Oklahoma tallgrass prairie. Prairie Naturalist 36:103–118.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411–1427.

Matsuda, H., P. A. Abrams and M. Hori. 1993. The effect of anti-predator behavior on exploitative competition and mutualism between predators. Oikos 68:549-559.

McCune, B., and D. Keone. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.

McNaughton, S. J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature 345:613–615.

McNaughton, S. J. 1992. The propagation of disturbance in savannas through food webs. Journal of Vegetative Science 3:301–314.

Mech, L. D. 1983. Handbook of animal radio-tracking. Universtiy of Minnesota Press, Mineapolis, Minnesota, USA.

Miller, W. 2002. Elk interactions with other ungulates. Pages 435–447 *in* D. E. Toweill and J. W. Thomas, Editors. North American elk: ecology and management. Smithsonian Institution Press, Washington D. C., USA.

Millspaugh, J. J., K. J. Raedeke, G. C. Brundige, and C. C. Willmott. 1998. Summer bed sites of elk (*Cervus elaphus*) in the Black Hills, South Dakota: considerations for thermal cover management. American Midland Naturalist 139:133–140.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing. Journal of Wildlife Management 64:994–1003.

Millspaugh, J. J. 1999. Behavioral and physiological responses of elk to human disturbances in the Southern Black Hills, South Dakota. Dissertation, University of Washington, Seattle, Washington, USA.

Mooring, M. S., D. D. Reisig, E. R. Osborne, A. L. Kanallakan, B. M. Hall, E. W. Schaad, D. E. Wiseman, and R. R. Huber. 2005. Sexual segregation in bison: a test of multiple hypotheses. Behaviour 142:897–927.

Nellemann, C., and M. G. Thomsen. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the Arctic Coastal Plain, Alaska. Arctic 47:361–367.

Putnam, R. 1986. Competition and coexistence in a multi-species grazing system. Acta Theriologica 31:271–291.

Putnam, R. 1988. The ecology of resource use. Pages 34–58 *in* R. Putnam, editor. The natural history of deer. Cornell University Press, Ithaca, New York, USA.

Putnam, R. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London, UK.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosytems? BioScience 54:755–766.

Romesburg, H. C. 1981. Wildlife science: gaining reliable knowledge. Journal of Wildlife Management 45:293–313.

Rosenstock, S. S., C. S. O'Brien, R. B. Waddell, and M. J. Rabe. 2004. Studies of wildlife water developments in Southwestern Arizona: wildlife use, water quality, wildlife diseases, wildlife mortalities, and influences on native pollinators. Research Branch Technical Guidance Bulletin No. 8, Arizona Game and Fish Department, Phoenix, AZ, USA.

Rosenstock, S. S., W. B. Ballard, J. C. Devos, Jr. 1999. Viewpoint: Benefits and impacts of wildlife water developments. Journal of Range Management 52:302–311.

Salford Systems. 2008. CART: tree-structured non-parametric data analysis. v. 6.0. [software] San Diego, California, USA.

Sartwell, J. 2000. Geographic Telemetry Model (GTM) v2.3.5. [software] Missouri Department of Conservation, Columbia, MO, USA.

Schmidt, S. L., and S. DeStefano. 1996. Impact of artificial water developments on nongame wildlife in the Sonoran Desert of southern Arizona.: 1996 annual report. Arizona Cooperative Fisheries and Wildlife Research Unit, University of Arizona, Tucson, AZ, USA.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.

Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. Journal of Applied Ecology 18:343–353.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37:789–795.

Shrestha, R., and P. Wegge. 2008. Habitat relationships between wild and domestic ungulates in Nepalese trans-Himalaya. Journal of Arid Environments 72:914–925.

Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. Journal of Wildlife Management 43:976–985.

Singer, F. J. 1979. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. Journal of Wildlife Management 43:437–444.

Singer, F. J., and J. E. Norland. 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canadian Journal of Zoology 72:1383–1394.

Smit, I. P., and C. C. Grant. 2009. Managing surface-water in a large semi-arid savanna park: effects on grazer distribution patterns. Journal for Nature Conservation 17:61–71.

Steinberg, D., and M. Golovnya. 2006. CART 6.0 User's Manual. Salford Systems, San Diego, California, USA.

Stewart, K.M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

Telfer, E. S., and A. Cairns. 1979. Bison-wapiti interrelationships in Elk Island National Park, Alberta. Pages 114–121 *in* M. S. Boyce and L. D. Hayden-Wing, editors, North American elk: ecology, behavior, and management. University of Wyoming, Laramie, WY, USA.

Thompson, M. J., R. E. Henderson, T. O. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. Wildlife Society Bulletin 17:287–290.

Van Vuren, D. H. 2001. Spatial relations of American bison (*Bison bison*) and domestic cattle in a montane environment. Animal Biodiversity and Conservation 24:117–124.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Woek, B. N. 2003. Demographics and space use of mule deer and white-tailed deer in Custer State Park, South Dakota. Thesis, University of Missouri, Columbia, Missouri, USA.

Wood, A. K. 1989. Comparative distribution and habitat use by antelope and mule deer. Journal of Mammalogy 70:335–340.

Wydeven, A. P., and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. Journal of Wildlife Management 49:805–813.

Wydeven , A. P. 1979. Food habits and ecological relationships of elk to other herbivores in Wind Cave National Park. Masters Thesis, Iowa State University, Ames, Iowa, USA.

Table 1. List of variables evaluated in CART analysis of habitat use of ungulate species in Custer State Park, SD.

Variable	Units
Distance to asphalt road	(m)
Distance to gravel road	(m)
Distance to two-track road	(m)
Distance to flowing water	(m)
Distance to intermittent stream	(m)
Distance to shrub patch	(m)
Distance to patch edge	(m)
Distance to burn	(m)
Distance to open area (canopy cover = 0)	(m)
Terrain ruggedness	surface ratio
Slope	%
Elevation	(m)
Aspect	none, north, south, east, west
Visibility	(m) to visible road
Habitat type	11 types
Habitat type	16 types
Stem density	trees per acre

Table 2. A priori hypotheses, subhypotheses and models used to evaluate habitat overlap among the ungulate assemblage in Custer State Park, SD, 1993-2008.

Hypothesis	Subhypothesis	Model
Forage	Spp. not important	$\beta_1$biomass + $\beta_2$shrub
	Spp. Important	$\beta_1$grass + $\beta_2$forb + $\beta_3$shrub
	Spp. diversity important	β_1(biomass×diversity) + $\beta_2$shrub
Water	--	β_1d_streams + β_2d_ponds + β_3d_intermittentstreams
Predator avoidance	--	$\beta_1$multistrata + $\beta_2$singlestrata + $\beta_3$tpa + β_4d_forest
Predictable disturbance	Visibility not important	β_1d_pavedrd + β_2d_humandisturbance
	Visibility important	β_1d_pavedrd + β_2d_humandisturbance + $\beta_3$visibility
Unpredictable disturbance	Visibility not important	β_1d_twotrackrd + β_2d_gravel + β_3d_trail
	Visibility important	β_1d_twotrackrd + β_2d_gravel + β_3d_trail + $\beta_4$visibility

Table 2. Continued.

Hypothesis	Subhypothesis	Model
Thermal	Veg structure w. height	$\beta_1$canopy + $\beta_2$tpa + $\beta_3$multistrata+ $\beta_4$singlestrata
	Veg structure w. size	$\beta_1$canopy + $\beta_2$tpa + $\beta_3$size1+ $\beta_4$size2 + $\beta_5$size3 + $\beta_6$size4 + $\beta_5$size5
	Topographical	$\beta_1$radiation + $\beta_2$heatload
Spatal niche	Patch edge density × forage diversity	$\beta_1$patchdensity + β_2(biomass×diversity) + $\beta_3$patchdensity×(biomass×diversity)
	Patch edge density × water density	$\beta_1$patchdensity + $\beta_2$waterdensity + $\beta_3$patchdensity×waterdensity
	Patch edge density × intermittent streams	$\beta_1$patchdensity + β_2d_intermittentstreams + $\beta_3$patchdensity×d_intermittentstreams

Table 3. Number of locations used per species and predictive success for each seasonal classification tree to predict species use by habitat features based on ungulate locations in Custer State Park, SD, 1993–2008.

	Number of locations						
Season	Bison female	Bison male	Elk	Pronghorn	Mule deer	White-tailed deer	Predictive success (%)
Fall	1829	68	3034	1709	0	0	63.7
Winter	2450	222	2419	2249	439	512	58.2
Spring	2685	458	2225	2697	1134	1299	62.8
Summer	2215	288	2364	2108	843	1086	70.3

Table 4. Actual and predicted species classes (%) and total locations for the classification tree to predict use by habitat features based on ungulate locations for the spring season in Custer State Park, SD, 1993–2008.

	Predicted class						
Actual class	Bison female	Bison male	Elk	Pronghorn	Mule deer	White-tailed deer	Total cases
Bison female	62.0	5.7	5.7	16.9	6.2	3.4	2685
Bison male	5.5	81.2	3.7	4.4	1.1	2.0	458
Elk	4.1	5.3	68.2	5.0	8.0	9.4	2225
Pronghorn	28.7	7.8	7.2	46.2	6.4	3.6	2697
Mule deer	5.1	1.8	7.8	3.9	71.3	10.1	1134
White-tailed deer	5.0	3.9	5.9	5.9	5.9	75.7	1299

Table 5. Actual and predicted species classes (%) and total locations for the classification tree to predict species use by habitat features based on ungulate locations for the summer season in Custer State Park, SD 1993–2008.

	Predicted class						
Actual class	Bison female	Bison male	Elk	Pronghorn	Mule deer	White-tailed deer	Total cases
Bison female	75.5	4.2	2.7	11.9	3.7	2.0	2215
Bison male	1.4	94.4	1.4	0.3	0.3	2.1	288
Elk	5.7	3.6	66.2	5.6	8.0	11.0	2364
Pronghorn	22.1	5.5	5.7	56.7	7.1	2.8	2108
Mule deer	1.4	1.9	5.6	3.3	81.5	6.3	843
White-tailed deer	2.8	3.6	6.0	2.6	5.0	80.1	1086

Table 6. Actual and predicted species classes (%), and total locations for the classification tree to predict species use by habitat features based on ungulate locations for the fall season in Custer State Park, SD, 1993–2008.

	Predicted class				
Actual class	Bison female	Bison male	Elk	Pronghorn	Total cases
Bison female	78.4	3.3	7.6	10.7	1839
Bison male	1.5	95.6	2.9	0.0	68
Elk	10.8	14.3	69.2	5.6	3034
Pronghorn	48.2	4.2	10.9	36.7	1709

Table 7. Actual and predicted species classes (%), and total locations for the classification tree to predict species use by habitat features based on ungulate locations for the winter season in Custer State Park, SD, 1993–2008.

	Predicted class						
Actual class	Bison female	Bison male	Elk	Pronghorn	Mule deer	White-tailed deer	Total cases
Bison female	56.4	4.2	5.4	24.3	5.3	4.2	2450
Bison male	5.9	82.0	5.0	1.8	2.7	2.7	222
Elk	8.1	11.7	49.6	8.8	9.4	12.4	2419
Pronghorn	26.1	4.6	4.3	58.7	4.5	1.7	2249
Mule deer	3.2	1.1	8.7	3.0	75.6	8.4	439
White-tailed deer	2.5	4.9	6.4	2.1	4.7	79.3	512

Table 8. Actual and predicted classes (%), and total locations for the classification tree to predict species use by habitat features based on ungulate locations for all seasons combined in Custer State Park, SD, 1993–2008.

	Predicted class						
Actual class	Bison female	Bison male	Elk	Pronghorn	Mule deer	White-tailed deer	Total cases
Bison female	67.1	4.5	5.3	16.4	4.1	2.6	9189
Bison male	4.2	86.0	3.3	2.4	1.2	2.0	1036
Elk	7.5	9.2	63.6	6.3	5.9	7.6	10042
Pronghorn	30.2	5.7	6.8	50.1	4.8	2.2	8763
Mule deer	3.5	1.7	7.2	3.5	75.6	8.5	2416
White-tailed deer	3.7	4.0	6.0	4.0	5.4	78.0	2897

Table 9. Parameter estimates and standard errors (in parentheses) for the best model to predict habitat overlap among ungulate species in Custer State Park, SD, during each season, 1993–2008..

	Maximum likelihood estimate (β)			
Parameter	Fall	Winter	Spring	Summer
Intercept	33.42 (0.25)	60.05 (0.19)	42.71 (0.20)	35.65 (0.21)
Patch edge density	1.30[a] (1.62)	-2.70 (0.27)	4.94 (0.20)	
Diversity-adjusted biomass	-0.95[a] (1.11)	-2.16 (0.48)		
Patch edge density × Diversity-adjusted biomass	6.64[a] (2.23)	1.61 (0.45)		
Distance to intermittent streams			-3.43 (0.20)	-3.50 (0.24)
Distance to ponds				1.03[a] (0.20)
Distance to streams				1.97 (0.25)

[a] = Non-linear, pseudo-threshold form of variable (ln(x+0.001)

Table 10. Mean and range of overlap index, and mean bias error (MBE) and root mean-squared error (RMSE) averaged across 3 cross-validation folds for each seasonal model to represent the hypothesis explaining habitat overlap among the ungulate assemblage in Custer State Park, SD, based on data collected 1993–2008.

Season	Range	Mean	MBE	RMSE
Summer	0.00–73.70	35.68	2.95 (2.28)	15.61 (0.26)
Fall	0.00–64.48	33.28	7.20 (2.46)	16.25 (1.25)
Winter	0.00–78.57	45.40	-0.60 (0.10)	17.71 (0.18)
Spring	0.00–74.88	42.68	0.03 (0.38)	17.10 (0.15)

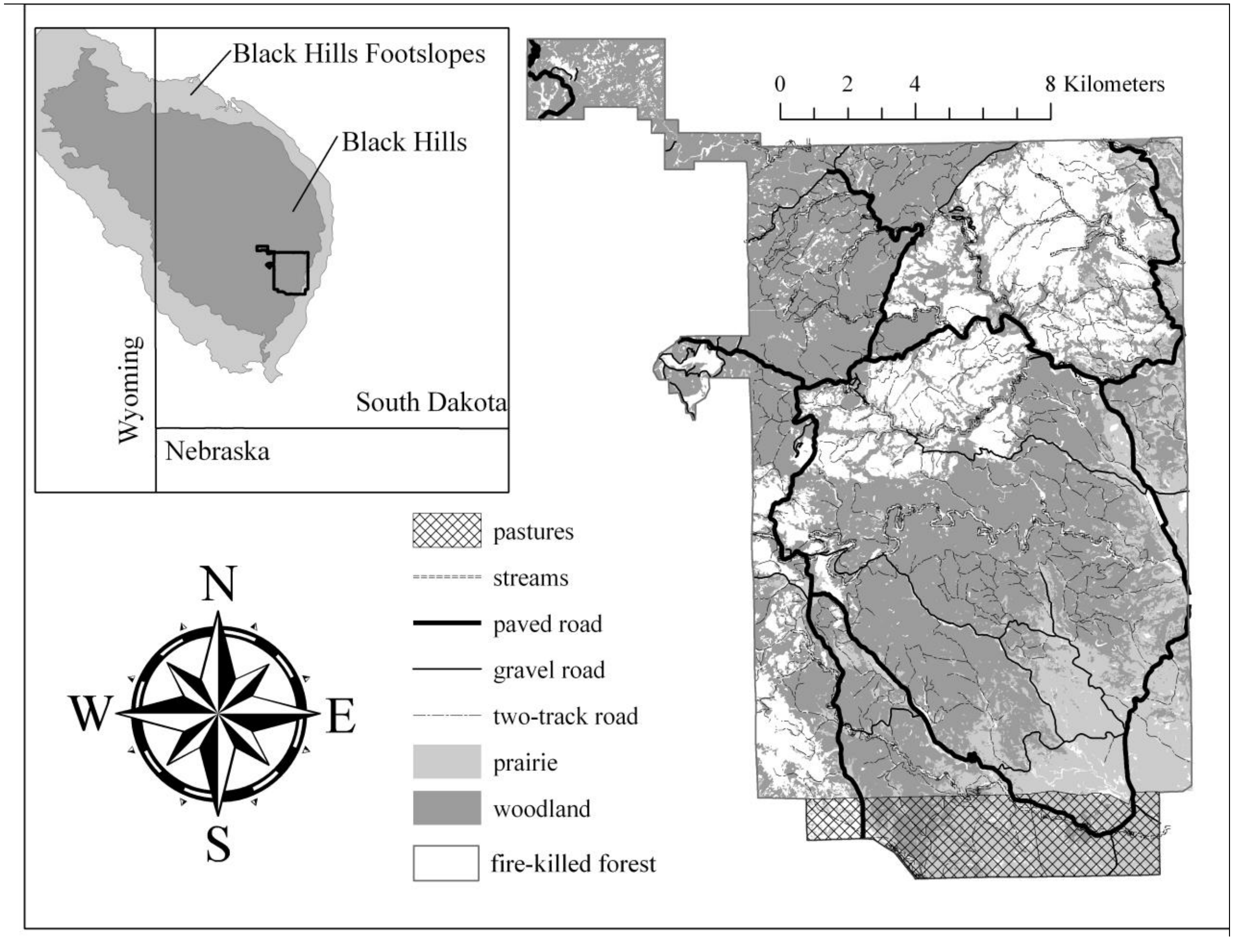

Figure 1. Major features and habitat types of Custer State Park, SD.

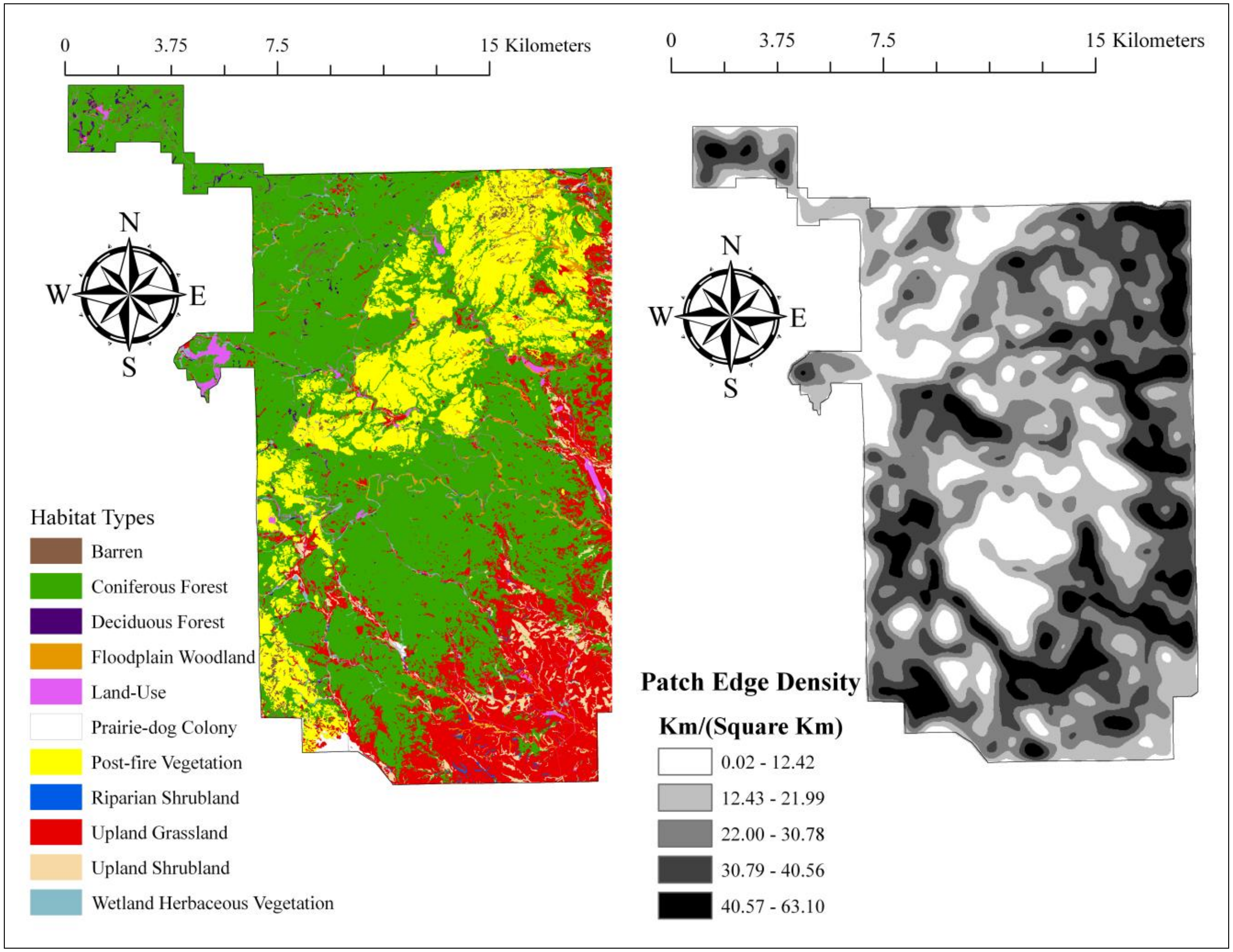

Figure 2. Major habitat types in Custer State Park, SD, based on aerial photography typing in Cogan et al. (2004; left), and density of edges (right) created from the habitat map.

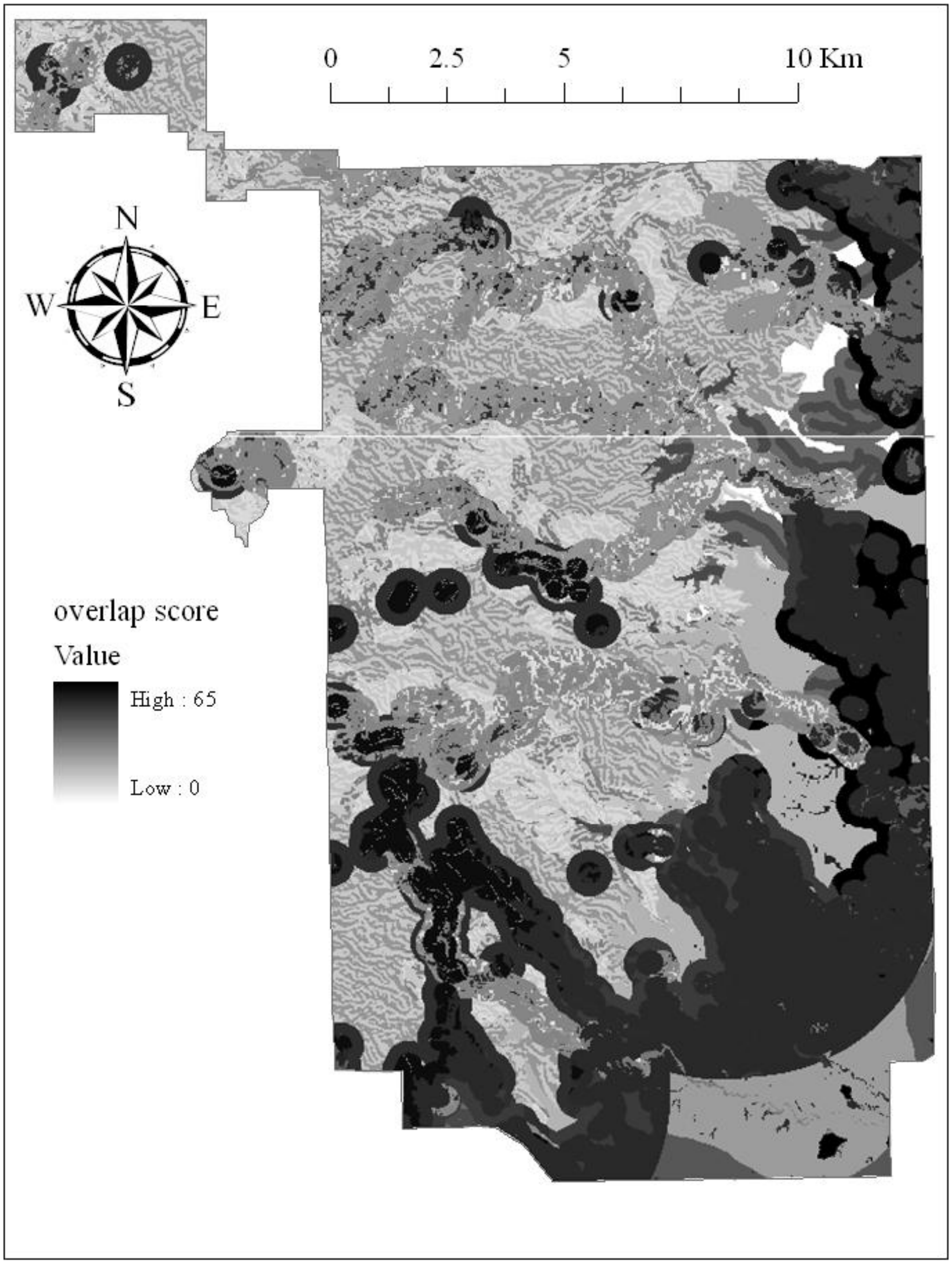

Figure 3. Habitat overlap among ungulates in Custer State Park, SD, during the fall, based on data collected 1993–2008.

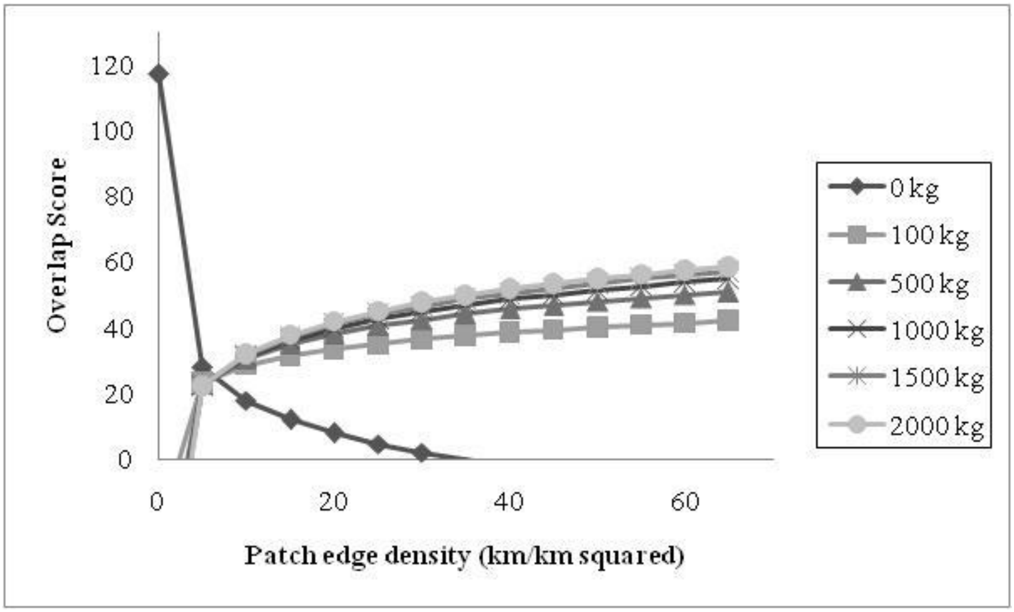

Figure 4. Response of spaital overlap to patch-edge density at differing levels of diversity-adjusted biomass for the ungulate assemblage in Custer State Park, SD, during the fall, based on data collected 1993–2008.

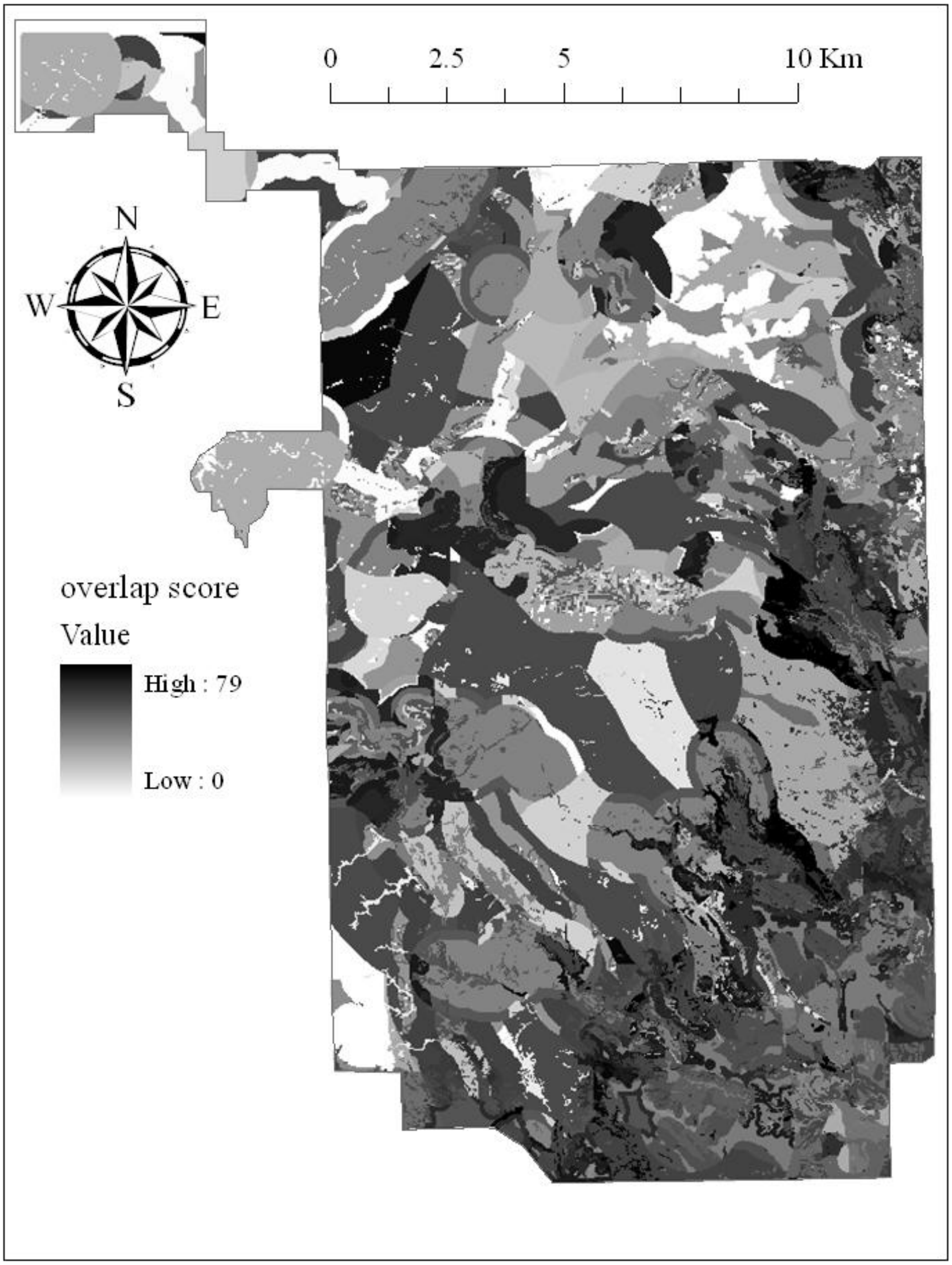

Figure 5. Habitat overlap among ungulates in Custer State Park, SD, during the winter, based on data collected 1993–2008.

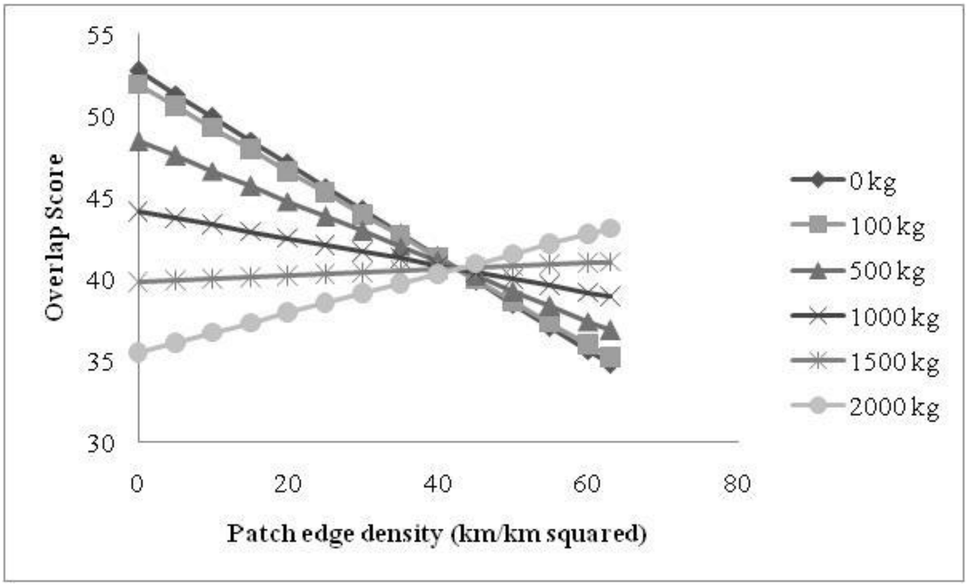

Figure 6. Response of habitat overlap score to patch-edge density at differing levels of diversity-adjusted biomass for an ungulate assemblage in Custer State Park, SD, during the winter, based on data collected 1993–2008.

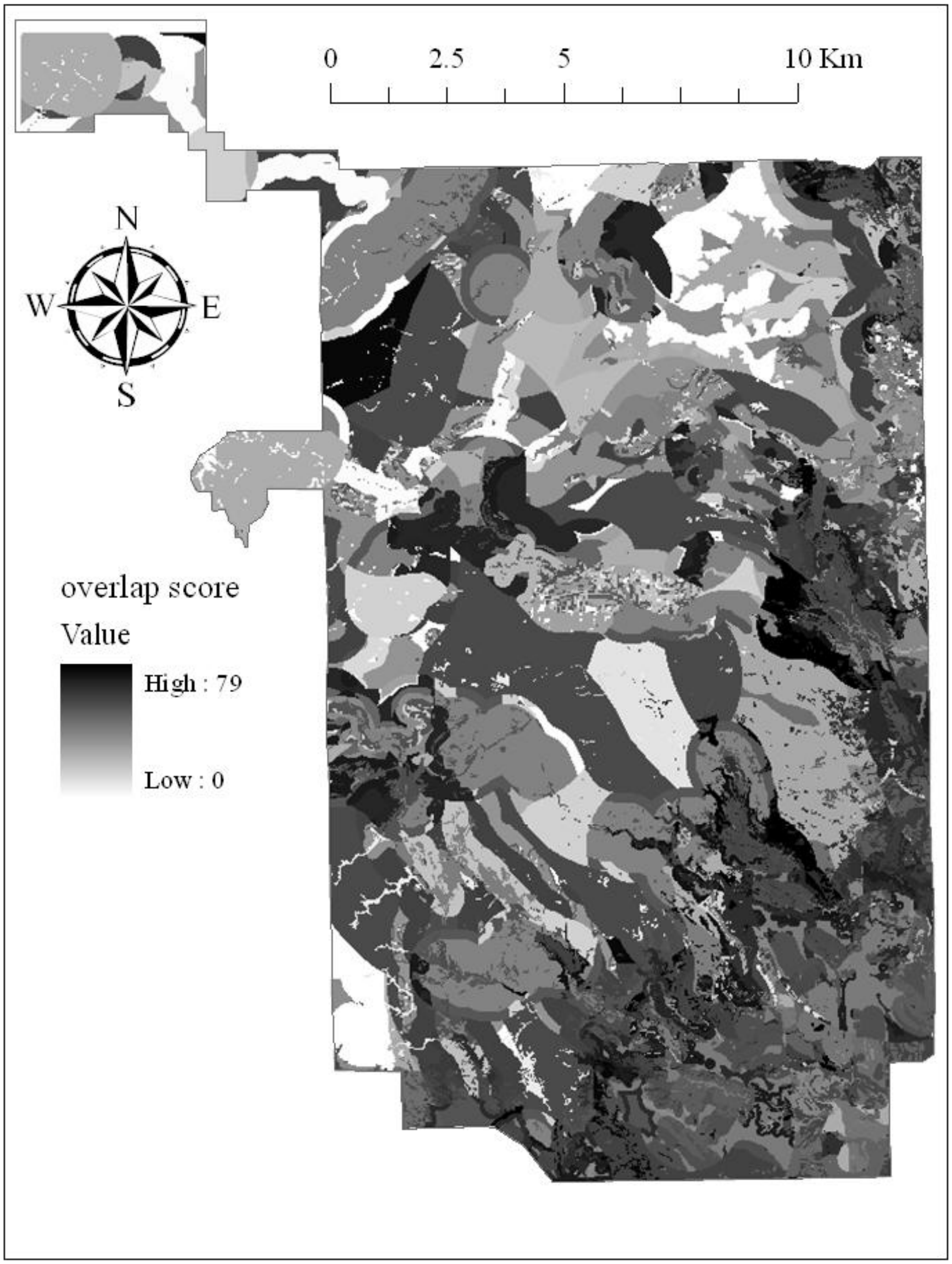

Figure 7. Habitat overlap among ungulates in Custer State Park, SD, during the spring, based on data collected 1993–2008.

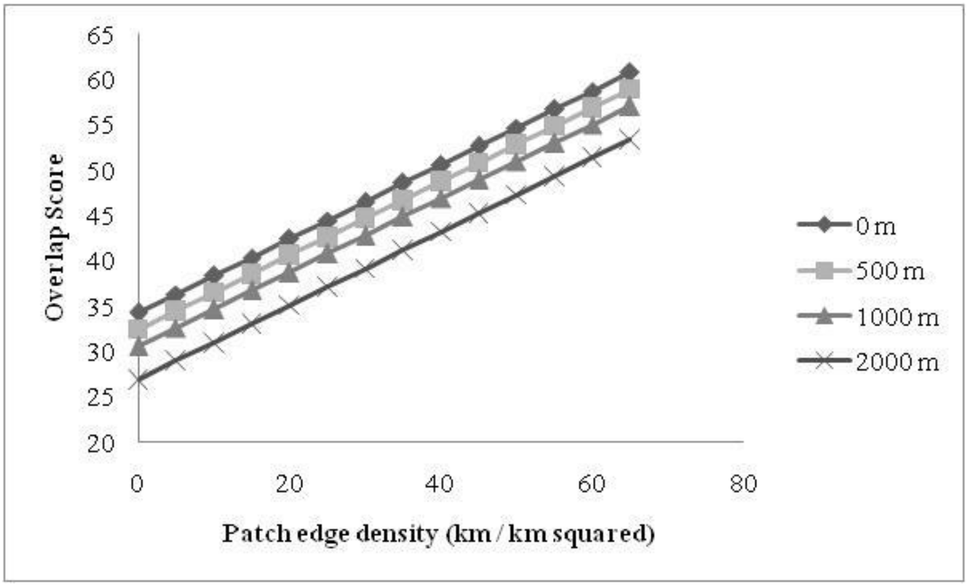

Figure 8. Response of habitat overlap score to patch-edge density at differing distances to intermittent streams for an ungulate assemblage in Custer State Park, SD, during the spring, based on data collected 1993–2008.

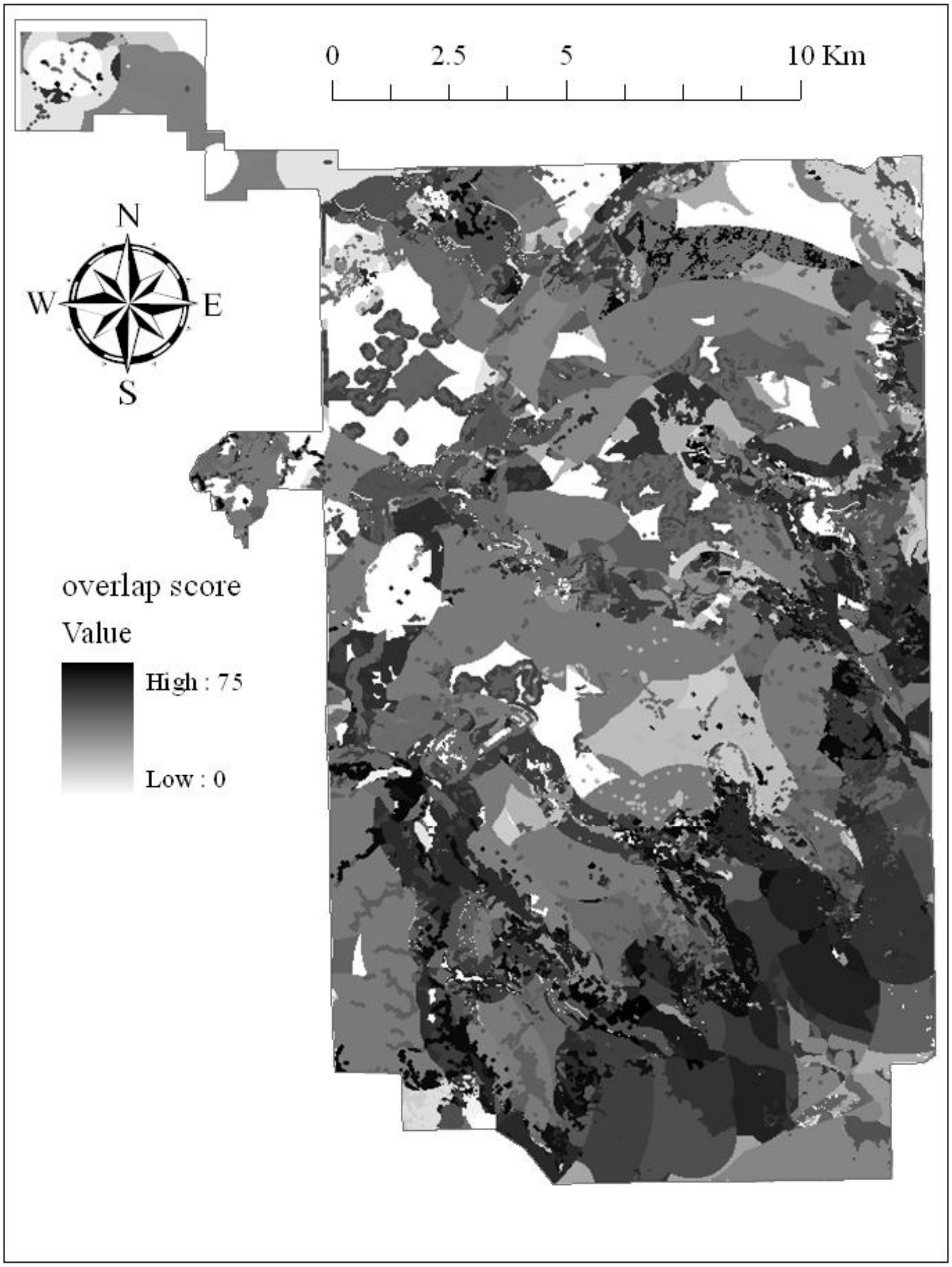

Figure 9. Habitat overlap among ungulates in Custer State Park, SD, during the summer, based on data collected 1993–2008.

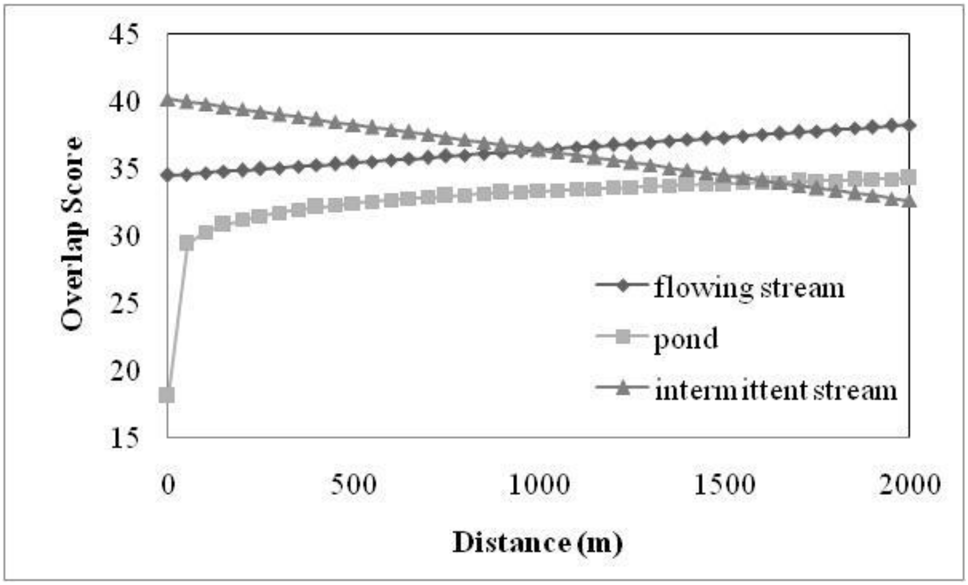

Figure 10. Response of habitat overlap score to distance to flowing streams, ponds, and intermittent streams, with other factors held constant, for an ungulate assemblage in Custer State Park, SD, during the summer, based on data collected 1993–2008.

CHAPTER VI. A SPATIALLY EXPLICIT FORAGE ALLOCATION MODEL FOR CUSTER STATE PARK, SOUTH DAKOTA

ABSTRACT

Determining the size and composition of ungulate communities that a landscape can support is difficult, especially when ungulate communities are diverse and explicit information on forage production and resource use of ungulates is lacking. Carrying capacity models can be useful tools to guide management decisions, however these models often make simplified assumptions about forage production, forage availability, and diet overlap. We used spatially-explicit information of forage production, diet selection, space-use, and habitat overlap of an ungulate assemblage in Custer State Park, SD, to develop a model that used linear optimization to optimize stocking densities of bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*). We removed the allowable use constraint and compared carrying capacity estimates from model runs that did, and did not, incorporate resource selection, habitat overlap, and diet overlap to determine the relative importance of these factors. We also used the model to evaluate forage utilization at current stocking densities during our study period. Seasonal carrying capacity estimates incorporating all factors were highest during the winter (2864 ungulates), intermediate during spring (1636 ungulates) and fall (1353 ungulates), and lowest during the summer (1012 ungulates). Our model optimized seasonal stocking densities at 25% allocation of total forage production at 500–659 bison, 212–699 elk, 100–584 mule deer, 100–795 white-tailed deer, and 100–541 pronghorn, that were

generally below current stocking densities for most species. Comparison of current stocking densities to forage production suggest utilization of many forage species may be above 25% but generally below 50%. The incorporation of resource selection greatly decreased carrying capacity estimates for some species. Total seasonal carrying capacity estimates that did not incorporate resource selection were 84–144% higher than those that did, and ignoring both spatial availability of forage and diet overlap among the ungulate community would result in total carrying capacity estimates 144 to 239% greater than when both of those factors are considered. In general, tradeoffs existed between maximizing bison and elk, elk and white-tailed deer, and pronghorn and mule deer populations. Coexistence of bison and elk populations was dependant on the availability of palatable grasses, while forbs and shrubs were important for white-tailed deer and elk, and mule deer and pronghorn. Forage species that our model indicated have a tendency to be overutilized at current stocking densities include big bluestem, blue grama, needleanthread, sedges, common yarrow, northern bedstraw, and woodland shrubs. Management actions that increase the biomass of these species would facilitate coexistence among the ungulate assemblage. Our results demonstrated the importance of incorporating diet overlap, habitat overlap, and resource selection in stocking density estimates, especially for large and diverse ungulate assemblages. The model we produced will be most useful to examine theoretical relationships related to stocking densitites and forage production, and tradeoffs in optimizing ungulate population numbers, rather than a strictly applied estimate of ungulate carrying capacities.

INTRODUCTION

Determining the number of ungulates a plant community can support is a central issue in wildlife and resource management. Resource managers at federal agencies, parks, and preserves often struggle to meet public demand for wildlife numbers while maintaining the integrity of the ecological community. Carrying capacity is broadly defined as the maximum number of animals that can be maintained in a given area on a long-term basis without habitat deterioration (Fritz and Duncan 1994). When managing several different ungulate species on one range, determining carrying capacity is complicated because many factors are involved and the ability of habitats to support ungulate populations changes temporally and under different grazing regimes (Frank et al. 2002).

Building a model to represent the ecological community can synthesize and organize all of the available information to estimate carrying capacity. Forage allocation models are used by wildlife managers to predict range condition and carrying capacity, and to facilitate management of ungulate populations to reach specific goals (Irby et al. 2002). Linear optimization models of forage allocation allow the rapid evaluation of management options before implementation on the ground, thus helping avoid unforeseen consequences while aiding in the justification of management decisions to the general public and federal officials (Westfall and Irby 1993, Irby et al. 2002).

The applicability of carrying capacity models to ungulate management has generally been confounded by unreasonable data requirements (digestibility and crude protein content of forage; Hanley and Rogers 1989), or a lack in spatial or temporal variability of the data collected (Irby et al. 2002). Nutritional carrying capacity models introduced by Hobbs and Swift (1985) and modified by Hanley and Rodgers (1989) used linear optimization models to predict the number of ungulates a range could support based on the nutritional requirements of the animal and the digestible energy and protein content of available forage. The advantage of modeling carrying capacity on a nutritional basis is that it allows for changes in diet composition as forage availability changes (Hanley and Rogers 1989). However, this approach strictly predicts the number of ungulates a range could nutritionally support if all of the available biomass was consumed, and does not incorporate spatial dynamics of ungulate resource selection. Furthermore, nutritional quality of plant species can differ due to temporal, topographical, climatic, and land use characteristics throughout an area of interest (Milchunas et al. 1995). Westfall and Irby (1993) developed a forage allocation model for Theodore Roosevelt National Park, in North Dakota, which did not incorporate the nutritional quality of the forage available, but attempted to incorporate coarse spatial estimates of forage production and resource use of ungulates. However, this model did not accurately predict the response of plant communities to ungulate grazing pressure or precipitation changes (Irby et al. 2002).

Carrying capacity models may also perform poorly due to a failure to account for diet and habitat overlap among all herbivores in a system and spatially-explicit resource selection. Most models are built for 1 species, assuming no diet or habitat overlap with other herbivores, and allocate the total amount of forage produced in the study area as available to the animal. This could result in an overestimation of carrying capacity because ungulates will likely not use all of the available forage on the landscape since it may be unpalatable, indigestible, or in areas that are inaccessible to the animal due to factors such as roads. A more realistic approach is to consider all ungulates that exist at a site and their spatial dynamics, which affects forage use and ultimately carrying capacity.

Custer State Park (CSP), located in the Black Hills of South Dakota, hosts several large ungulate species, including elk (*Cervus elaphus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis canadensis*) and pronghorn (*Antilocapra americana*). Tourism associated with wildlife viewing is an important source of revenue for CSP (CSP 1995); bison and pronghorn are especially important because they are easily viewed during daylight hours, from vehicles, and during most weather conditions. Resource managers currently estimate range carrying capacity using a conventional model incorporating precipitation levels, National Resource Conservation Service (NRCS) estimates of forage production per soil type, and assumptions of the diet preference and resource selection of ungulates present. The original allocation model was developed 30–50 years ago for elk, bison and domestic horses in CSP (G. Brundige, personal communication). These models were refined during the later part of this initial period to include refined production estimates for range sites and were applied to elk, bison and “other grazers.” Additional refinements were made in the early 1990’s to include estimates of woodland production based on soil and overstory characteristics. Forage production estimates and resource utilization by ungulates remain untested.

We incorporated spatially explicit data on diet and habitat selection of ungulates, diet and habitat overlap among ungulates, and forage production in CSP into a linear optimization forage allocation model. To develop this model, we measured actual forage production and developed a spatially explicit GIS layer of forage production, resource selection, and habitat overlap of all ungulates in CSP. We estimated carrying capacity under a variety of allowable forage removal values and for normal, favorable, and unfavorable forage production years, as dictated by environmental conditions. We compared carrying capacity estimates from model runs that did and did not incorporate resource selection, habitat overlap, and diet overlap to assess the importance of these factors. We also compared actual stocking densities to model simulations based on forage production predicted for conditions during our study period.

STUDY AREA

Custer State Park encompasses 286.32 km^2 in southwest South Dakota, approximately 27 km southwest of Rapid City. Custer State Park is composed of a mixture of rangeland and forest common to the southern Black Hills region. Steep granite spires characterize the northwest portion of the Park, undulating forested hills dominate the central portion, and grasslands dominate the eastern and southern portions of the Park (CSP 1995; Figure 1). Elevations range from 1,146–2,042 meters (CSP 1995).

Over half (55%) of CSP is covered by forest. The central forested portion of CSP is dominated by ponderosa pine (*Pinus ponderosa*) which shifts to a mixture of ponderosa pine and white spruce (*Picea glauca*) on northern slopes and high elevations (Figure 1). A small amount of deciduous forest (2% of CSP) is characterized by predominantly bur oak (*Quercus macrocarpa*) and quaking aspen (*Populus tremmuloides*) forest occurs primarily in riparian corridors (Figure 1). Stand structure diversity in CSP consists of 52.33 km^2 of single-story forest and 71.49 km^2 of multi-story forest (CSP 1995). Woodland understory communities in CSP are dominated by

Kentucky bluegrass (*Poa pratensis*), poverty oatgrass (*Danthonia spicata*), sedges (*Carex* spp.), bearberry (*Arctostaphylos uva-ursi*), wild raspberry (*Rubus ideaus*), and western snowberry (*Symphoicarpus occidentalis*; Custer State Park, unpublished data). Almost 30% of CSP is burned-over forest, results of the Galena fire of 1988, the Cicero Peak fire of 1990, and the Four-mile fire of 2008. Fire-damaged forest consists of 84.79 km^2, 60% of which is fire-killed where nominal regeneration has occurred and where the canopy remains open (CSP 1995; Figure 1).

Approximately 21% (61.05 km^2) of CSP is northern mixed-grass prairie and upland shrubland (CSP 1995; Figure 1). Grasslands are dominated by Kentucky bluegrass, big bluestem (*Andropogen gerardi*), little bluestem (*Andropogen scoparius*), western wheatgrass (*Agropyron smithi*), blue grama (*Bouteloua gracilis*), and sideoats grama (*Bouteloua curtipendula*; CSP 1995). Common shrub species include leadplant (*Amorpha canscens*), western snowberry, wild raspberry, and wild rose (*Rosa* spp.). Approximately 28,499,216 kg of palatable forage is produced in an average year in CSP (Chapter 1).

Thirteen watersheds occur either completely or partially within the Park (CSP 1995). There were 6 streams with constant annual flow and numerous ephemeral and permanent water impoundments in CSP during our study period (Figure 1). Water impoundments were created in the prairie region specifically for use by bison and other wildlife, or were already present when CSP was created from old ranching operations. Four large reservoirs are present in CSP, although two of these are outside of the fenced portion of the park and unavailable to bison. The other two reservoirs are located outside of the prairie region. There were two solar-driven water troughs located in the prairie region during the study period that provided a constant supply of fresh water for wildlife, and 69 other small permanent and ephemeral ponds. The maximum and average distance to a water source in CSP was 2.73 and 0.69 km, respectively.

For 1992–2008, annual precipitation for CSP averaged 49.86 cm and ranged from 74% to 161% of the 25-year mean. Approximately 76% of precipitation in CSP fell from April to September (Custer State Park, unpublished data). Winter in the southern Black Hills is considerably milder than elsewhere in the region, and a persistent snowpack was not typically present during the study period. Average snowfall for the southern Black Hills is 32.0 cm; March is the snowiest month with an average snowfall of 18.8 cm. Temperatures in CSP are more moderate than the surrounding plains; the average annual, summer and winter temperature in CSP is 6.7° C, 16° C, and –5° C, respectively (CSP 1995).

Approximately 800–1000 bison, 408–1126 elk, 98–279 pronghorn, 867 white-tailed deer, 285 mule deer, 38–200 bighorn sheep, and 35–40 feral burros (*Equus asinus*) occupied CSP during our study period (C. Lehman, Custer State Park, personal communication). Bison are culled annually during the fall bison roundup, as well as during several hunts in the fall. Coyotes (*Canis latrans*), mountain lions (*Felis concolor*) and bobcats (*Felis rufus*) are the major predators in CSP. Wolves (*Canis lupus*) and grizzly bear (*Ursus arctos*) populations native to the region have been extirpated. A 1.54 m woven-wire fence surrounds the majority of the CSP except for a small portion of the Park in the Needles and Sylvan Lake area. This fence prevents movement of bison but allowed for movement of all other ungulate species into or out of CSP, although movement of ungulates out of the park is rare (CSP, unpublished data). There are three other internally fenced areas in CSP, which create three distinct pastures in CSP and are used to move bison during the roundup and to manage grazing of bison throughout the year (Figure 1).

There is a considerable amount of human-related infrastructure in CSP, consisting of paved, gravel, and two track roads and numerous buildings and campgrounds. There are 90.1 km of paved roads, including two state highways, and 76.5 km of gravel roads open to the public, in CSP. Two-track roads, which are only used by park employees, cover 560.9 km. There are approximately 84 small structures and buildings in the park, six campgrounds, and one small airport. From 2005–2008, an average of 1,631,432 people visited CSP annually. The majority of this visitation (59%) occurred during the summer, followed by fall (20%), spring (16%) and winter (5%; C. Pugsley, Custer State Park, personal communication).

METHODS

We used linear optimization to determine allocation of forage production among ungulate species in CSP. Linear optimization is the process of determining the maximum or minimum mathematical function given certain constraints. The optimal solution is the function that meets goals of the objective function without violating the constraints. Optimization models are widely used in fields involved in decision making and provide a useful tool for viewing the effects of certain management strategies before implementation (Walters and Hilborn 1978).

Linear optimization models are composed of 5 components: the objective function, the controllable inputs, uncontrollable inputs, constraint variables, and the optimal solution (Figure 2). The objective function is the mathematical function subject to constraints. For our model, the objective function was to maximize efficient use of forage production among all 5 ungulate species while incorporating spatial components of forage production and habitat selection by each ungulate species. Controllable inputs are the set of decision variables that affect the value of the objective function, and uncontrollable inputs are parameters associated with the problem. Controllable inputs in this model were the population size of each ungulate species. These are factors that the model manipulates to reach the optimal solution. The uncontrollable inputs were sex and age composition of each ungulate population, daily dry matter intake, and diet selection of each ungulate species. The model cannot change these inputs to reach a solution. The constraint variable allows the decision variables to take on certain values and exclude others. The constraint variables for our model were the total amount and species composition of forage production that was spatially available to each ungulate species. The optimal solution was the optimal mix of the maximum number of controllable inputs that completely utilize the most limiting constraint without over-utilizing it. In our case, the optimal solution was the numbers of each ungulate species that can be supported given the total forage production (Figure 2).

There are 4 assumptions in linear optimization: certainty (no variances around the parameter inputs), linearity (the functions driving the variables are linear), non-negativity (all decision variables > 0), and additivity (contribution of each ungulate is mutually exclusive and is not affected by contributions of other ungulates). However, the certainty, linearity, and additivity assumptions could not be reliably met. Our parameter inputs were means that do have variances associated with them, we could not assume the relationships among many of these biological factors is linear, and there was most likely additivity occurring in the foraging decisions of the ungulates. However, certainty rarely occurs in ecology, we will never now actual total forage production for CSP, or the actual diet selection of the entire ungulate assemblage. Trying to measure these parameters to 100% certainty would be time and cost-prohibitive, if not impossible. Most ecological models are based parameters that are estimated from field data, and because this model is intended to be used as a tool, not as an absolute truth, we are comfortable violating the certainty assumption. We are simplifying the relationship of the true ecological community by ignoring the linearity and additivity assumptions. Thus the estimated optimal solution from our model is assuming that the linearity and additivity assumptions are met, which is typical in forage allocation models based on linear optimization (Westfall and Irby 1993, Kuzyk et al. 2009).

This optimization model was a modified version of the forage allocation model developed by Westfall and Irby (1993) for Theodore Roosevelt National Park. The objective function was:

$$MAX \sum_{J=1}^{4} X_J$$

where X_j = numbers of ungulates (X_1 = white-tailed deer, X_2 = mule deer, X_3 = elk, X_4 = pronghorn, and X_5 = bison). The model expands to:

$$Z = aX_j \quad \text{or} \quad Z = aX_1 + aX_2 + aX_3 + aX_4 + aX_5$$

where Z = The solution to the objective function and a = the objective function coefficient.

The objective function was subject to constraints that took the form of the inequality:

$$\sum_{J=1}^{4} D_{IJ} R_J X_j \leq U_I S_i$$

where D_{ij} = proportion of the ith plant species grazed by the jth animal species; R_j = daily dry matter intake of the jth ungulate species (g/day); U_i = allowable Use Factor (AUF) of the ith forage species; and Si = total production (kg) of ith forage species allocated to each ungulate species. The constraints expand to the formats:

$$(D_{1,1}\ T\ R_1) + (D_{1,2}\ T\ R_2) + \ldots. \leq U_1\ S_1$$

$$(D_{2,1}\ T\ R_1) + (D_{2,2}\ T\ R_2) + \ldots. \leq U_2\ S_2$$

$$(D_{3,1}\ T\ R_1) + (D_{3,2}\ T\ R_2) + \ldots. \leq U_3\ S_3$$

$$\text{etc.} \qquad + \qquad \text{etc.} \qquad + \ldots. \leq \text{etc.}$$

where T = season and

$$AX_1 + BX_2 + CX_3 + DX_4 + EX_5 \leq AF$$

where A–E = coefficients of ungulate species representing the rate at which a typical animal will consume a forage species, and AE = the amount of forage allocated to all ungulate species in the grazing area.

There were 4 major inputs to this model: (S_i) = amount of forage that was produced that was spatially available to each ungulate species for consumption and adjusted for habitat overlap among other ungulate species with similar diet compositions; (U_i) = percent allowable use of each forage species; (D_{ij}) = diet composition of each ungulate species; and (R_j) = daily intake rate of the jth ungulate species (kg/day).

Diet composition

We used data on seasonal diet composition of each ungulate species obtained from microhistological analysis of feces (Chapter 4).

Spatially-available forage production

In order to determine the amount of forage spatially available to each ungulate species, we needed information on resource selection of each species and spatially explicit forage production. We used a spatially-explicit forage production model developed by Keller (Chapter 1), which includes parameters for range and woodland grazable site, slope, elevation, canopy cover, prairie dog colony, current annual spring precipitation, previous year spring precipitation, and ordinal date of last spring frost. This model explained 40% of the variation in forage biomass in CSP, and produced similar estimates to transect-based sampling when applied to Wind Cave National Park, directly south of CSP (Keller and Millspaugh 2010).

We used resource selection models developed by Woeck (2003) for elk, white-tailed deer and mule deer resource selection, and models we developed separately for bison (Chapter 2) and pronghorn resource selection (Chapter 3). Woeck (2003) used logistic regression to evaluate characteristics of used and available resources of deer and elk within the study area (i.e., second-order selection; Johnson 1980). We used the summer (mid-April to August) models from Woeck (2003) to represent spring resource selection and winter models (January to mid-April) to represent fall resource selection for elk, white-tailed deer and mule deer, because Woeck did not evaluate spring and fall resource selection. These models are listed in Appendix II.

We separated resource selection probabilities for each species and season into 3 categories: high, mid, and low probability of use, based on natural breaks in the resource selection values for each species. We rescaled resource selection maps for areas of high, mid- and low use to 1.0, 0.5, and 0, respectively. We multiplied these modified resource selection maps by the spatially-explicit forage production map to determine forage availability for each species for each season. In this way, only half (0.5 × total forage production) of the forage production in areas of mid-use by an ungulate species was available to that species, while all (1.0 × total forage production) of the forage in areas of high use, and none (0.0 × total forage production) of the forage in areas of low use was available to that species.

We further modified available forage by habitat overlap among ungulate species. We only adjusted available forage for ungulate species that had a Schoener's (1968) dietary overlap value ≥ 0.50 with any other ungulate species for any season (see Chapter 4). This was a conservative cut-off because Schoener's index of overlap is considered to be biologically significant when ≥ 0.60 (Schoener 1968, Ross 1968). During all seasons, dietary overlap between elk and bison, and white-tailed deer and elk exceeded 0.50. During spring, significant dietary overlap also occurred between pronghorn and mule deer, and white-tailed deer and mule deer. During summer, significant dietary overlap also occurred between pronghorn and elk, white-tailed deer and pronghorn, and pronghorn and mule deer. During fall, ungulate species pairs with significant dietary overlap included white-tailed deer and pronghorn, and mule deer and white-tailed deer. During winter, mule deer and pronghorn also overlapped significantly in diet composition.

For species pairs with significant dietary overlap, we adjusted forage availability in areas where probability of occurrence was mid or high for each of the species (Table 1). We allocated forage among species pairs based on *a priori* knowledge of the competitive abilities of ungulates (Table 2). By "competitive ability" we mean that one of the two species has an advantage over the other species with regards to the consumption of forage species that the two species both utilize. We assumed bison had a slight competitive advantage over elk, as these species overlapped in grass consumption and bison are more efficient at the consumption of large amounts of low quality grass than are elk (Hoffman and Stewart 1972, Putman 1988). We also assumed that elk had a competitive advantage over white-tailed deer where the species overlapped in space-use. There is actually little literature available regarding the competitive interactions of these two species (Miller 2002). However, the competitive advantage of elk over mule deer has been widely reported (Mackie 1970, Collins and Urness 1983, Lindzey et al. 1997, Johnson et al. 2000, Stewart et al. 2002), and we hypothesized this relationship would extend to the closely-related white-tailed deer. We assumed that all other overlap between ungulates would compete equally in use of forage species where they overlapped in space, although those areas were still adjusted by the probability of selection for each ungulate species. This new overlap-adjusted forage availability (Table 2) was used to determine the proportion of forage in each range and woodland site that was available to each ungulate species per season (Tables 3–6).

Allowable forage use

This percentage can change depending upon the forage species, but was set at 25% for our purposes. Most range managers only allocate 50% or less of the total production of any species to allow for trampling, to leave an appreciable amount of forage on the landscape for fall and winter use, and to maintain the ecological integrity of the rangeland (Holechek et al. 2004).

Daily intake rate of the *j*th ungulate species

This was determined from the available literature on ungulate nutritional requirements. We used birth weight estimates from Robinette et al. (1973) for mule deer and unpublished yearling and adult weight estimates for mule deer collected from the Black Hills (Theresa Zimmerman, South Dakota State University, unpublished data; Table 7). We used data on white-tailed deer birth, yearling and adult weights from Schmitz (2006) and unpublished sources (Theresa Zimmerman, South Dakota State University, unpublished data; Table 8). For white-tailed and mule deer juveniles, we estimated daily weight gain per day by using the difference between birth weight and yearling weights, and averaged the weights for each 90-92 day seasonal period. We obtained herd composition data for white-tailed deer and mule deer in CSP from Woeck (2003; Table 8). We used linear equations published in Martin and Parker (1997) to estimate weights of pronghorn fawns per day, and averaged the weights for each 90-92 day seasonal period (Table 9). We used weight estimates for adult and yearling pronghorn published in (O’Gara 2004) and Mitchell (1971). Seasonal dry matter intake rates for pronghorn were obtained from Yoakum (2004). We used unpublished data on average CSP bison weights (Chad Kremer, Custer State Park, unpublished data; Table 10), herd composition, and obtained estimates of bison birth weight and daily intake rates from Fiest (2000). We estimated weight of bison calves per day using daily weight gain estimates from Fiest (2000), and averaged the weights for each 90-92 day seasonal period (Table 10). We obtained birth weights of elk from Smith et al. (1997) and projected weight gain per day with estimates from Cook (2002; Table 11). We used weight estimates for adult and yearling elk from Cook (2002). We assumed elk and bison lose 10% of their normal body weight over winter (Fiest 2000, Cook 2002).

We assumed the birth date for the juveniles of each species to be March 1 to estimate juvenile weights per season. This was certainly a simplification as most ungulates do not give birth until later during the summer months. Bison, however, do typically bear young during April and May in CSP (B. Keller, unpublished data). Elk and both deer species typically give birth in early summer and pronghorn give birth during the later summer months in CSP. However, juveniles consume relatively little forage compared to adults so this assumption likely played little importance in the stocking density calculations.

Linear optimization model

We used the Solver add-in in Microsoft Excel (2007) to model our linear optimization function. The above inputs were compiled in tabular format for each ungulate and major forage species. We set lower bounds for population sizes of 500 for bison, 300 for elk, and 100 for pronghorn, white-tailed deer, and mule deer populations for model runs and used forage production based on the 25-year mean of climatic values. We asked the model to maximize the total population of all ungulates in the park. If minimum population constraints were not met, we determined forage species that were limiting population sizes of ungulates and removed them if they composed <5% of the diet of the species. If allowable use of a forage species was preventing minimum population constraints to be met, we increased allowable use based on the amount of that species in ungulate diets and ecological importance of the species. Once the minimum constraints of the model were for 25% allocation of available forage, we also evaluated stocking density estimates at 35% and 50% allocation, using the same constraints regarding allowable use or availiability of forage species we relaxed for the 25% allocation. We also estimated seasonal carrying capacity for favorable conditions, using spring precipitation 150% of normal and an early date of last spring frost (20 April), and unfavorable conditions, using spring precipitation 50% of normal and a late date of last spring frost (25 May) to predict forage production. We compared carrying capacity estimates incorporating resource selection and diet and habitat overlap to what estimates would be if these factors were not incorporated into the calculation, we did not incorporate allowable use constraints during these model runs because we were only interested in relative changes in carrying capacity estimates. We evaluated the limiting constraints for the population sizes of each ungulate species for each season. Finally, we evaluated the total consumption of forage using average stocking densities of each ungulate species and average forage production during our study period. We used population sizes of 553 elk, 285 mule deer, 867 white-tailed deer and 215 pronghorn for every season, and 900 and 1250 bison for winter-spring and summer-fall, respectively (G. Brundige, Custer State Park, unpublished data).

RESULTS

Spring carrying capacity

Spring carrying capacity was intermediate between winter and fall. The model predicted a carrying capacity of 600 animals for spring, but did not meet the minimum constraints of 500 bison or 300 elk. Based on a sensitivity analysis to determine what forage species were limiting elk and bison, we found that prairie sandreed (*Calamovilfa longifolia*) was constraining the bison population and little bluestem (*Schizachyrium* *scoparium*) was constraining the elk population, and combined sedge (*Carex* spp.), cheatgrass (*Bromus tectorum*) and needleandthread consumption was greater than 25% of total seasonal production. We eliminated prairie sandreed and little bluestem constraints from bison and elk population estimation and increased allowable use of sedge and needleandthread to 35% and allowable use of cheatgrass to 100%, and re-ran the model. Praire sandreed and little bluestem comprised 1.7 and 0.8% of bison and elk diets during spring, respectively, thus we felt comfortable removing these constraints. Cheatgrass is considered an invasive exotic species (Larson and Johnson 1999), thus we allowed 100% consumption given CSP staff would not be concerned with conservation of the species, and we were comfortable increasing allowable use of needleandthread and blue grama to 35% as this is still considered a conservative grazing allotment (Holechek et al. 2004). These modifications resulted in a successful model run that met all constraints. The model optimized carrying capacity for CSP during the spring for 25% allocation of most forage species at 1635 animals, consisting of 500 bison, 698 elk, 100 mule deer, 100 white-tailed deer, and 237 pronghorn. The binding constraints of the model were the amount of indianwheat (*Plantago patagonica*) available to pronghorn, and the total allowable use of indianwheat and needleandthread (*Stipa comata*). At 35% allocation of forage species, carrying capacity increased to 1780 individuals, and at 50% allocation it increased to 2801 individuals (Table 12). For a favorable climatic year, the model maximized carrying capacity at 7108 animals, consisting of 500 bison, 4299 elk, 364 mule deer, 100 white tailed deer and 1854 pronghorn. For an unfavorable climatic year, the model maximized summer carrying capacity at 617 animals, consisting of 17 bison, 300 elk, 100 mule deer, 100 white-tailed deer and 100 pronghorn.

Summer carrying capacity

Summer carrying capacity was lowest compared to all other seasons. The model predicted a carrying capacity of 599 ungulates, but did not meet the constraints of a minimum population of 500 bison, 300 elk, or 100 mule deer. We found that total consumption of blue grama (*Bouteloua gracilis*) and prairie sandreed were greater than 25% and that the availability of little bluestem and wild rose to elk were limiting the model. To meet minimum constraints, we increased allowable use of these species to 35% for blue grama and 60% for prairie sandreed. We felt comfortable increasing blue grama to 35% because this is still considered a conservative grazing rate (Holecheck et al. 2004), and increasing prairie sandreed to 60% because it composed such a small amount of any wildlife diets (Chapter 4). We increased prairie sandreed to this amount because it was the lowest allowable use that would meet the constraint. We eliminated the little bluestem constraint from elk population estimation, which composed 2.4% of summer elk diets. However, we were not comfortable eliminating the wild rose constraints for the elk population, because this species composed 9.4% of summer elk diets. These modifications resulted in a successful model run for bison, mule deer, white-tailed deer, and pronghorn, but not elk, and the model predicted a total carrying capacity of 1012 for 25% allocation of most forage species, consisting of 500 bison, 212 elk, 100 mule deer, 100 white-tailed deer, and 100 pronghorn. Carrying capacity increased to 1367 individuals at 35% allocation and 1731 individuals for 50% allocation (Table 12). The binding constraints of the model were the allowable use of common yarrow (*Achillea millefolium*), prairie sandreed, and wild rose (*Rosa* spp.). For a favorable climatic year, the model maximized carrying capacity at 4375 animals, consisting of 2140 bison, 300 elk, 1115 mule deer, 180 white-tailed deer, and 639 pronghorn. For an unfavorable climatic year, the model maximized summer carrying capacity at 278 animals, consisting of 141 bison, 0 elk, 100 mule deer, 36 white-tailed deer and 0 pronghorn.

Fall carrying capacity

Fall carrying capacity was higher than summer, but less than winter and spring. The fall carrying capacity model maximized stocking density at 826 animals, but it did not meet the minimum population size constraints for bison or elk. We found the amount of little bluestem and mountain mahogany available to elk, and the total allowable use of cheatgrass, mountain mahogany, and skunkbrush (*Rhus aromatica*) to be constraining the model. Little bluestem and mountain mahogany composed 2.3 and 0.8% of fall elk diets, respectively. Thus, we eliminated the little bluestem and skunkbrush constraint from the elk, and increased allowable use of cheatgrass, mountain mahogany and skunkbrush to 100%. We believe our estimate of skunkbrush and mountain mahongany production to be underestimated (see Chapter 1), and thus increased it to this amount, and as mentioned above, cheatgrass is not a desired species in CSP. This resulted in a successful model run, which maximized carrying capacity at 1353 animals, consisting of 659 bison, 337 elk, 100 mule deer, 157 white-tailed deer, and 100 pronghorn. The binding constraints for the fall carrying capacity model were the available production of mountain mahogany (*Cercocarpus montanus*) to elk, as well as the total allowable use of indianwheat and needleandthread. Carrying capacity increased to 1771 and 1955 individuals at 35 and 50% allocation, respectively (Table 12). For a favorable climatic year, the model maximized fall carrying capacity at 4971 animals, consisting of 2979 bison, 337 elk, 1232 mule deer, 323 white-tailed deer, and 100 pronghorn. For an unfavorable climatic year, the model maximized fall carrying capacity at 395 animals, consisting of 176 bison, 101 elk, 71 mule deer, 47 white-tailed deer and 0 pronghorn.

Winter carrying capacity

Winter carrying capacity was highest compared to all other seasons. The winter carrying capacity model predicted a carrying capacity of 860 animals, but did not meet the minimum population size constraints for elk. The only limiting constraint was the amount of little bluestem and mountain mahogany available to elk. Little bluestem and mountain mahogany composed 2.0 and 0.9% of winter elk diets, respectively, thus we removed this constraint and ran the model again. The model ran successfully, and maximized carrying capacity at 2863 animals, consisting of 644 bison, 300 elk, 583 mule deer, 795 white-tailed deer, and 541 pronghorn. The binding constraints of this model included allowable use of common yarrow, fringed sagewort (*Artemisia frigida*), ponderosa pine (*Pinus ponderosa*), and sand dropseed (*Sporobolus cryptandrus*). Carrying capacity increased to 4006 individuals at 35% allocation and increased to 5306 individuals at 50% allocation of forage species (Table 12). For a favorable climatic year, the model maximized winter carrying capacity at 12966 animals, consisting of 2749 bison, 548 elk, 5306 mule deer, 3394 white-tailed deer, and 968 pronghorn. For an unfavorable climatic year, the model maximized winter carrying capacity at 562 animals, consisting of 174 bison, 88 elk, and 100 mule deer, white-tailed deer and pronghorn.

Carrying capacity without resource selection or overlap

The removal of resource selection and diet overlap constraints had a large influence on total carrying capacity estimates. Seasonal carrying capacity estimates that did not incorporate resource selection were 84–144% higher than those that did (Table

13). However although total carrying capacity estimates were always higher, some species-specific carrying capacity estimates did not change or actually decreased when resource selection was removed from the model, because the model found it could optimize the total population size by allocating forage to other species once the resource selection constraint was removed. Ignoring both spatial availability of forage and diet overlap among the ungulate community would result in total carrying capacity estimates 144 to 239% greater than when both of those factors are considered. Almost all species-specific carrying capacity estimates increased markedly when both resource selection and diet overlap constraints were removed from the model (Table 13) with the exception of white-tailed deer estimates during the summer and elk estimates during the fall. Both the white-tailed deer estimate during the summer and the elk estimate during the fall were constrained by the total amount of skunkbrush produced in CSP, which is why these estimates did not increase.

Tradeoffs in increasing species numbers

Species that appear to be competing with one another in CSP include bison and elk, mule deer and pronghorn, and white-tailed deer and elk. Elk and bison numbers, in particular, were a problem for our carrying capacity model as the minimum population constraint was often violated during the initial model runs. Elk compete with both bison and white-tailed deer for forage and space in CSP, which likely confounded linear optimization model. Mule deer and pronghorn populations also appeared to limit each other, although the minimum population of pronghorn was always supported. White tailed deer did not appear constrained by forage production and other ungulate populations in CSP during winter or summer.

Evaluation of current stocking densities

Estimates of winter stocking densities for the ungulate assemblage in CSP appear to be within carrying capacity, although total use of some forage species may be greater than 25%. During winter, our model indicated there was adequate forage available to support the average stocking density of 900 bison, 215 pronghorn, and 285 mule deer. However, it indicated that there was not enough available little bluestem, mountain mahogany and northern bedstraw to support 553 elk and not enough ponderosa pine to support 867 white-tailed deer. The above species are very minor components of elk diets in CSP (Chapter 4), thus the stocking density of 553 elk is not likely to be a problem. We also believe our production estimate of ponderosa pine to be underestimated (Chapter 1), so this species is not likely to limit white-tailed deer populations. Most forage species were within the allowable use allotment at these stocking densities, with the exception of common yarrow (40.7%), indianwheat (45.9%), Kentucky bluegrass (25.2%), mountain mahogany (227.8%), needleandthread (26.4%), northern bedstraw (51.2%), ponderosa pine (34.2%), wild rose (33.3%), sand dropseed (42.2%), and western wheatgrass (31.1%).

The stocking density of bison and mule deer may be slightly higher than carrying capacity during spring based on our model, and the total amount of some key forage species, including big bluestem, blue grama, and needleandthread may be higher than allotted. Our model indicated that there was only enough forage to meet the stocking density for pronghorn. The stocking density of elk was only limited by available little bluestem, which as discussed above, is not likely to be a problem for elk populations, thus the stocking density of 553 elk appears to be within spring carrying capacity. The amount of cheatgrass, needleandthread, prairie sandreed, and sedge available to bison was inadequate to meet current stocking densities for spring. However, of the above factors, only needleandthread and sedge are likely to be important to bison populations based on their diet composition during spring (Chapter 4). The model indicated bison needed to access 34% more needleandthread and 37% more sedges to meet forage intake for spring. There were not adequate amounts of indianwheat and rose available to support current densities of mule deer. Indianwheat only accounts for 0.8% of spring mule deer diets, but wild rose accounts for 7.5% of mule deer spring diets. Mule deer would need to access to 27% more wild rose to meet current stocking densities. White-tailed deer did not have adequate amounts of indianwheat and common yarrow at current stocking densities, but these are minor components of white-tailed deer diets during spring (Chapter 4). Forage species that were grazed at greater than 25% allowable use during spring included big bluestem (31.9%), blue grama (31.5%), cheatgrass (67.1%), common yarrow (25.7%), indianwheat (121.7%), needleandthread (57.9%), prairie sandreed (102.5%), and sedge (59.7%). Decreasing the stocking density of bison to 700 would meet reasonable available forage requirements and decrease use of big bluestem to 26.6% and blue grama to 24.9%. However needleandthread and sedges would be grazed at 47.6 and 49.6% of total production, respectively.

Our model indicated none of the current stocking densities of ungulates during summer could be met by available forage and 25% allowable use. There was not enough blue grama, cheatgrass, green muhly (*Muhlenbergia racemosa*), needleandthread, prairie sandreed, sedge, or timothy available to bison to support current densities. However, the only above species that constitute an appreciable amount of bison diets during summer are blue grama (19.7%), needleandthread (5.5%), and sedges (18.3%). Our model indicates bison would need access to 28.9% more blue grama, 63.7% more needleandthread, and 204.5% more sedges to meet these stocking densities. There was not an adequate amount of common yarrow, leadplant, little bluestem, and wild rose available to elk to meet the current stocking density. Of the above, only leadplant and wild rose compose > 5% of elk diets during summer (Chapter 4). Our model indicates elk would need access to 50.0% more leadplant and 365.0% more wild rose to meet current stocking densities. The only forage species that was not in adequate supply to meet the stocking density of pronghorn was indianwheat, which only composes 0.4% of pronghorn diets during summer. The amount of wild rose available to mule deer was a problem at current stocking densities, our model indicated mule deer needed access to 360% more wild rose. White-tailed deer did not have access to adequate amounts of aspen, common yarrow, indianwheat, wild rose, or skunkbrush at current stocking densities. However, only wild rose accounts for an appreciable amount (20.0%) of white-tailed deer diets during summer. White-tailed deer would need to access 316.3% more wild rose than is currently available to the species based on our model. Species that were grazed at higher than 25% allowable use during summer included big bluestem (38.2%), blue grama (81.2%), cheatgrass (60.6%), common yarrow (99.6%), indianwheat (79.1%), needleandthread (52.4%), prairie sandreed (121.9%), wild rose (99.5%), sedges (60.3%), sideoats grama (36.7%), and western wheatgrass (27.4%). We found acceptable stocking densities to be 650 bison, 400 elk, and current densities of mule deer, white-tailed deer, and pronghorn. This stocking combination met most of the forage requirements of bison and elk and decreased total utilization of big bluestem, blue grama, needleandthread, sedges, and western wheatgrass to within reasonable limits (all < 50%).

During fall, our model indicated current stocking densities could only be adequately supported for mule deer in CSP. Bison did not have adequate access to blue grama, cheatgrass, and needleandthread biomass to meet the stocking density of 1250 individuals. However, only blue grama and needleandthread are major components of bison diets during fall (Chapter 4), bison would need access to 9.7% more blue grama and 34.3% more needleandthread to support this stocking density. Our model indicates inadequate amounts of little bluestem, mountain mahogany, and skunkbrush to meet elk forage requirements during fall. However, all of these species are only minor components (<5%) of fall elk diets (Chapter 4). There was not enough indianwheat available to pronghorn at current stocking densities, but this species only accounts for 1.9% of pronghorn diets during the fall (Chapter 4). The amount of indianwheat, oak (*Quercus* spp.), raspberry, and wild rose was inadequate to meet the forage needs of white-tailed deer under current stocking densities. Of these forage items, only raspberry and rose composed >5% of white-tailed deer diets. White-tailed deer would need access to 80.4% more raspberry and 193.6% more wild rose to meet forage requirements at current stocking densities. Forage species that were grazed at higher than 25% allowable use during spring included big bluestem (36.7%), blue grama (50.4%), cheatgrass (83.2%), green needlegrass (39.4%), indianwheat (98.3%), Kentucky bluegrass (41.9%), mountain mahogany (224.2%), needleandthread (56.8%), northern bedstraw (46.3%), wild rose (55.4%), sedges (44.8%), skunkbrush (260.2%), and western wheatgrass (43.2%). We found decreasing the population of bison to 1000 individuals met reasonable available forage requirements and decreased the total use of most grass species to within acceptable limits (<50%). We also decreased the white-tailed deer stocking density to 600 individuals, but left the other stocking densities of ungulates at the default values.

Carrying capacity of individual species

Bison population estimates appear to be constrained by the amount of certain grasses, including sand dropseed, prairie sandreed, needleandthread, cheatgrass, and sedge that are spatially available to them. However, sand dropseed, prairie sandreed, and cheatgrass compose such small amounts of bison diets during any season (Chapter 4) that these constraints on bison populations are not realistic, while needleandthread and sedge are more likely to limit the population. However, the allowable use of certain forage species was also an important constraint. During the winter, fall, and summer bison are constrained by the allowable use of blue grama. The allowable use of western wheatgrass and needleandthread is also important during the winter and fall, respectively. The allowable use of needleandthread and sedge constrained bison populations during spring.

Elk population estimates were constrained by the amount and allowable use of certain grasses and forbs. Little bluestem was a particularly important species constraining elk population estimates, the amount of spatially available little bluestem constrained elk population estimates during all seasons. However, this species comprised <2.8% of elk diets during any season, so it is not likely to limit elk populations. The only other graminoid that constrained elk populations was the allowable use of sedge during the spring, which is an important forage species to both bison and elk during this season

(Chapter 4). The allowable use of forbs including northern bedstraw, indianwheat, and common yarrow, were limiting constraints on elk populations during all seasons.

The three concentrate selectors, mule deer, pronghorn, and white-tailed deer, were constrained by forb and shrub species. The amount of spatially-available and allowable use of rose was an important factor limiting the population estimates of mule deer during all seasons, white-tailed deer during the fall, summer, and spring, and pronghorn during the fall and summer. Fringed sagewort was a constraint limiting both pronghorn and mule deer population estimates. The allowable use of leadplant is the first constraint for mule deer populations during the winter. Other forage species that limited the population estimate of white-tailed deer included ponderosa pine during the winter, raspberry during the fall, skunkbrush during winter, and common yarrow and northern bedstraw during spring.

DISCUSSION

Our forage allocation model revealed potential tradeoffs with maximizing population sizes of each species and identified forage species that have the potential to be overutilized at current stocking densities and biomass production. Given current conditions and stocking densities in CSP, our model indicated that it is not likely that all forage species are grazed at less than 25% allocation. Ungulates may be removing more than range managers had accounted for because the previous allocation model did not include empirically-based, spatially-explicit information on habitat overlap, resource selection, and diet overlap, However, most forage species were not utilized over 50%, which is still considered a conservative amount of removal for range managers (Holechek et al. 2004). Increases in the number of one ungulate species generally affected other ungulate numbers, suggesting resource partitioning in the ungulate assemblage is not complete. In general, tradeoffs existed between maximizing bison and elk, elk and white-tailed deer, and pronghorn and mule deer populations. Coexistence of bison and elk populations was dependant on the availability of palatable grasses, while forbs and shrubs were important for white-tailed deer and elk, and mule deer and pronghorn. Management actions that increase biomass of these forage species may facilitate coexistence of competing ungulates.

Our forage allocation model optimized stocking densities of CSP ungulates that differed substantially from current stocking densities. Given the goal of the linear optimization program, to maximize the total number of ungulates on the landscape while meeting certain constraints, this result is not surprising. Our model does not rank gain in any one ungulate as superior over any other, thus an increase in one white-tailed deer is treated the same as one bison, and because smaller ungulates consume less forage than larger ungulates in the park, the model (all other factors held equal) will favor adding several smaller ungulates to the population versus one large ungulate. However, there are certainly differences in the value from wildlife viewing, hunting, and other activities among the ungulate assemblage. Custer State Park is known world-wide for its large bison population, and this is considered one of the main attractions of the park. Thus, managers are going to value adding bison to the ungulate assemblage over most other ungulate species. Kuzyk et al. (2009) also found large differences in optimized stocking densities predicted by a forage allocation model for Elk Island National Park, Canada, and actual stocking densities due to similar issues with linear optimization. We recommend managers change the optimal solution of the model to maximize the most valued species in the park, perhaps bison, elk and pronghorn, while maintaining a minimum population size of other ungulate species to more closely simulate management goals.

The seasonal trend in carrying capacity estimates we observed reflected the changes in nutritional requirements in ungulates. Carrying capacity estimates were greatest during the winter when ungulate intake rates are depressed and animals typically lose weight, and lowest during the spring and summer when females have greater nutritional requirements due to lactation and gestation (Robbins 1993, Cook 2002). This is a key difference between nutritional carrying capacity techniques, which compare forage quality to nutritional requirements of ungulates, and biomass-based carrying capacity techniques, which compare forage intake rates and diet composition of ungulates to available biomass. Generally winter carrying capacity estimates are lowest relative to other seasons because the nutritional quality of the forage does not typically meet the nutritional requirements of the ungulate (Wallmo et al. 1977, Hobbs et al. 1982). However, because forage intake rates are typically depressed during winter and animals lose body weight, carrying capacity estimates based on forage biomass predict higher carrying capacity during winter relative to other seasons. It is likely that ungulate diets we observed during winter did not meet nutritional requirements, and thus carrying capacity estimates during this time are overestimates. Spring, summer and fall are important periods for ungulates to gain fat reserves that sustain them during periods of nutritional restriction (Mautz 1978). Thus, managers should focus on the minimum carrying capacity estimates during the spring and summer as a conservative estimate of carrying capacity.

Our model demonstrated that wildlife managers working with large and diverse ungulate assemblages should not disregard diet overlap, habitat overlap, and resource selection in stocking density estimates. In most cases, incorporating these factors in our forage allocation model markedly decreased carrying capacity estimates for each ungulate species. Thus, carrying capacity may be over-estimated if these factors were not considered, potentially leading to rangeland degradation. However, these factors are typically ignored in carrying capacity calculations. For example, elk are sympatric with mule or white-tailed deer throughout most of their range (Miller 2002), however nutritional carrying capacity estimates published by Wallmo et al. (1977), Hobbs et al. (1982), and Beck et al. (2006) for elk or deer in areas where the species overlap did not account for potential competition. Although moose (*Alces alces*) are sympatric with white-tailed deer in Quebec, Canada, Potvin and Huot (1983) did not consider moose foraging effects in their estimates of white-tailed deer carrying capacity for the area. Kuzyk et al. (2009) suggested their reported lower carrying capacities for the ungulate assemblage in Elk Island National Park in Canada compared to Telfer and Scotter (1975) is due to including deer species in the model calculations that Telfer and Scotter excluded. The need to incorporate diet and habitat overlap in carrying capacity estimates obviously becomes more important as the number of species coexisting in any area increases, but given wild ungulates share much of their range with domestic livestock (Fleischner 1994), it should be considered in most wild ungulate populations.

In general, differential habitat selection within a study area is also widely ignored in the calculation of carrying capacity. We found incorporating resource selection to determine the amount of forage that was spatially available to each ungulate generally decreased the carrying capacity estimates, particularly of bison and pronghorn. The common practice is to simply consider all of the forage in any specific area as available to an animal, as in Wallmo et al. (1977), Hobbs et al. (1982), Hobbs and Swift (1985), Hanley and Rogers (1989), McLeod (1997), Bothma et al. (2004), and Kuzyk et al. (2009). However, abundant literature indicates ungulate avoidance of certain features, such as areas associated with human activity (Stephenson et al. 1996, Rowland et al. 2000, Dyer et al. 2001, Nelleman et al. 2001, Cole et al. 2004) and attraction to other features such as water sources, mineral sites, and preferred foraging areas (McNaughton 1988, VerCauteren et al. 2007, Schuler et al. 2006, Smit and Grant 2009). One notable exception is Beck et al. (2006), who found incorporating habitat selection probabilities in nutritional carrying capacity calculations for elk in Nevada to decrease carrying capacity estimates. It is possible that failing to incorporate the above factors in carrying capacity calculations may account for one reason the general poor performance of carrying capacity models in the past (McLeod 1997).

Our model uses a novel approach to carrying capacity estimation in that we incorporated spatially explicit forage production by species, and diet selection, diet overlap, resource selection, and habitat overlap of each ungulate species. However, there are a number of assumptions built into our model, that as with any ecological model, limits its application. Our model is deterministic and does not incorporate stochasticity or variability of forage production, animal intake rates, weights, or diet. However, an advantage of our model compared to those developed by Westfall and Irby (2002) and Kuzyk et al. (2009) is the ability to predict spatially-explicit forage production based on the specific climatic conditions of each year. Thus, although we are not able to account for stochasticity within annual forage production, we can account for yearly variation in forage production due to weather. We are also unable to account for compensatory growth of vegetation in response to grazing (Pastor et al. 1997), thus our carrying capacity estimates are likely conservative.

Further, it is important to highlight the potential drawbacks of using resource selection (Boyce and McDonald 1999) and resource utilization function models (Marzluff et al. 2004) to project potential use of ungulate species on the landscape. Although we had adequate locations for each species to develop species-wide utilization distributions (Samuel et al. 1985), the disparate resource selection studies in CSP spanned several years, which requires an important assumption. By projecting the resource selection and utilization models on the landscape we assume that the manner in which each species selects those resources has remained constant over time. We accounted for differences in landscape attributes when building models, but application of those models assumes the resource selection patterns remained static over time. Further, resource selection models might predict use in certain areas because of suitable habitat, yet the species might not occur there. This is not a limitation of our approach, rather any resource selection model can identify suitable environments that a species might never use for a variety of reasons. However, we believe this assumption is more valid than assuming utilization distributions by each of the 5 ungulate species would remain constant over 15 years of data collection.

Our model may place undo emphasis on diet composition. We assume that diet is constant, and does not change due to variation in climate or other factors, which is likely untrue. We further assume that the diets we measured for each ungulate species in Chapter 2 adequately met nutritional requirements. It is likely that diet switching

(Coomes et al. 2003) occurs, and that certain forage species are interchangeable so that if one species is grazed to the maximum available another forage species may be substituted. Further, it might be useful to eliminate those forage species that compose less than 5% of ungulate diets from the model completely, as these species tended to constrain ungulate populations to lower levels than current stocking densities. It might be more appropriate to combine forage species into functional groups, such as ‘warm-season bunchgrasses’, ‘cool-season bunchgrasses’, ‘warm-season annual grasses’, etc. Such groupings would loosen the emphasis on specific forage species, which would likely be more appropriate for generalist herbivores such as bison and elk.

We simplified seasonal forage production in CSP by dividing total forage production by 4 for each season. This is a gross generalization; warm- and cool-season grasses and forbs vary in availability (Sims and Singh 1978) and palatability (Cogswell and Kamstra 1976) throughout the year on the mixed-grass prairie. We likely unduly constrained some ungulate population estimates by misrepresenting the availability of certain forage species throughout the year. Further, plant species composition will vary in response to climatic factors and to grazing intensity (Coppedge et al. 1998), which we are unable to account for with our forage production model. However, any model is an approximation of reality and must strike a balance between abstraction and intricacy (Starfield 1997), as the natural world is infinitely complicated. By highlighting and acknowledging the above assumptions and limitations of our model, we hope to facilitate and encourage use of this model as one of many tools CSP managers use to evaluate management actions, and not the sole basis for decision-making.

MANAGEMENT IMPLICATIONS

Our model would prove most useful, not to produce exact numbers to manage ungulate populations, but to use in conjunction with manager knowledge of the system, real-time field data, and past trends in ungulate and forage communities to help guide management actions. The most appropriate application of our model should consider the relative changes in numbers rather than apply numbers in an absolute sense. We emphasize that the model should be used to examine theoretical relationships related to stocking densitites and forage production, and tradeoffs in optimizing ungulate population numbers, rather than a strictly applied estimate of ungulate carrying capacities. Rather than asking the model to optimize stocking densities, managers could simply input current densities to determine proportional take of current forage production and forage species that may be overutilized. Our model predicted estimates of ungulate stocking rates generally fell below current stocking densities and this result is due to the assumptions we described above. Managers may consider removal of forage by the ungulate assemblage might be above 35% for some forage species, especially in years with lower than normal spring precipitation. It might be prudent to monitor plant species that were most sensitive to increases in ungulate populations. Forage species that our model indicated have a tendency to be overutilized at current stocking densities include big bluestem, blue grama, needleanthread, sedges, common yarrow, northern bedstraw, and woodland shrubs. Management actions that increase the biomass of these forage species would facilitate coexistence among the ungulate assemblage. We also recommend monitoring of woodland shrubs to better determine production of these species, as the population estimates of white-tailed deer, mule deer and pronghorn depend upon these production estimates.

LITERATURE CITED

Beck, J. L., J. M. Peek, and E. K. Strand. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. Journal of Wildlife Management 70:283–294.

Bothma, J. P., N. van Rooyen, and M. W. van Rooyen. 2004. Using diet and plant resources to set wildlife stocking densities in African savannas. Wildlife Society Bulletin 32:840–851.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Cogswell, C., and L. D. Kamstra. 1976. The stage of maturity and its effect upon the chemical composition of four native range species. Journal of Range Management 29:460–463.

Cole, E. K., M. D. Pope, and R. G. Anthony. 2004. Influence of road management on diurnal habitat use of Roosevelt elk. Northwest Science 78:313–321.

Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer ranges. Journal of Wildlife Management 47:646–663.

Cook, J. G. 2002. Nutrition and food. Pages 259–350 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington D. C., USA.

Coomes, D. A., R. B. Allen, D. M. Forsyth, and W. G. Lee. 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. Conservation Biology 17:450–459.

Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. Effects of seasonal fire, bison grazing, and climatic variation ono tallgrass prairie vegetation. Plant Ecology 139:235–246.

CSP. 1995. Custer State Park resource management plan 1995–2010. Unpublished document.

Dyer, S. J., J. P. O’Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65:531–542.

Feist, M. 2000. Basic nutrition of bison. Saskatchewan Agriculture and Food Extension Research Unit, Saskatoon, Saskatchewan, Canada.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Frank, D. A., M M. Kuns, and D. R. Guido. 2002. Consumer control of grassland plant production. Ecology 83:602–606.

Fritz, H., and P. Duncan. 1994. On the carrying capacity for large ungulates of the African savanna ecosystems. Proceedings Biological Sciences 256:77–82.

Hanley, T. A., and J. J. Rogers. 1989. Estimating carrying capacity with simultaneous nutritional constraints. Research Note PNW-RN-48. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen-based estimates of elk winter-range carrying capacity. Journal of Wildlife Management 46:12–21.

Hobbs, N. T. and D. M. Swift. 1985. Estimates of carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.

Hofmann, R. R., and D. R. Stewart. 1972. Grazer or browser? a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226–240.

Holechek, J. L., R. D. Pieper, and C. H. Herbel. 2004. Range management: principles and practices. 5th Edition, Person Education, Inc. Upper Saddle River, New Jersey, USA.

Irby, L. R., J. E. Norland, J. A. Westfall, and M. A. Sullivan. 2002. Evaluation of a forage allocation model for Theodore Roosevelt National Park. Journal of Environmental Management 64:153–169.

Johnson, B. K., J. W. Kern, M. J. Wisdon, S. L. Findholt, and J. G. Kie. 2000. Resource selection of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Keller, B. J., and J. J. Millspaugh. 2010. A forage allocation model for Wind Cave National Park. Final report submitted to Wind Cave National Park, Hot Springs, South Dakota.

Kuzyk, G. W., N. L. Cool, E. W. Bork, C. Bampfylde, A. Franke, and R. J. Hudson. 2009. Estimating economic carrying capacity for an ungulate guild in western Canada. The Open Conservation Biology Journal 3:24–35.

Lindzey, F. G., W. G. Hepworth, T. A. Mattson, and A. F. Reeve. 1997. Potential for competitive interactions between mule deer and elk in the Western United States and Canada. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, Wyoming, USA.

Mackie, R. J. 1970. Range ecology and relations of mule deer, elk and cattle in the Missouri River breaks, Montana. Wildlife Monographs 20:1–79.

Martin, S. K., and K. L. Parker. 1997. Rates of growth and morphological dimensions of bottle-raised pronghorns. Journal of Mammalogy 78:23–30.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Stellar's jays. Ecology 85:1411–1427.

Mautz, W. W. 1978. Sledding on a brushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88–90.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environments? Oikos 79:529–542.

McNaughton, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature 334:343–345.

Milchunas, D. G., A. S. Varnamkhasti, W. K. Lauenroth, and H. Goetz. 1995. Forage quality in relation to long-term grazing history, current year defoliation, and water resources. Oecologia 101:366–374.

Miller, W. 2002. Elk interactions with other ungulates. Pages 435–448 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington D. C., USA.

Mitchell, G. J. 1971. Measurements, weights, and carcass yields of pronghorns in Alberta. The Journal of Wildlife Management 35:76–85.

Nellemann, C., I. Vistnes, P. Jordhoy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biological Conservation 101:351–360.

O'Gara, B. W. 2004. Physiology and genetics. Pages 231–273 *in* B. W. O'Gara and J. D. Yoakum, eds., Pronghorn: ecology and management. University Press of Colorado, Boulder, Colorado, USA.

Pastor, J., R. Moen, and Y. Cohen. 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. Journal of Mammalogy 78:1040–1052.

Potvin, F., and J. Huot. 1983. Estimating carrying capacity of a white-tailed deer wintering area in Quebec. Journal of Wildlife Management 47:463–475.

Putman, R. 1988. The Natural History of Deer. Cornell University Press, Ithaca, New York, USA.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, Inc., San Diego, California, USA.

Robinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37:312–326.

Ross, S. T. 1968. Resource partitioning in fish assemblages: a review of field studies. Copeia 1986:352–388.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.

Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711–719.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726.

Schmitz, L. E. 2006. Ecology of white-tailed deer in South Dakota: growth, survival and winter nutrition. Dissertation, South Dakota State University, Brookings, South Dakota, USA.

Schuler, K. L., D. M. Leslie, J. H. Shaw, and E. J. Maichak. 2006. Temporal-spatial distribution of American bison (*Bison bison*) in a tallgrass prairie fire mosaic. Journal of Mammalogy 87:539–544.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands: II. Intra-seasonal dynamics in primary producer compartments. Journal of Ecology 66:547–572.

Smit, I. P., and C. C. Grant. 2009. Managing surface-water in a large semi-arid savanna park: effects on grazer distribution patterns. Journal for Nature Conservation 17:61–71.

Smith, B. L., R. L. Robbins, and S. H. Anderson. 1997. Early development of supplementally fed, free-ranging elk. Journal of Wildlife Management 61:26–38.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261–270.

Stephenson, T. R., M. R. Vaughn, and D. E. Anderson. 1996. Mule deer movements in response to military activity in southeast Colorado. Journal of Wildlife Management 60:777–787.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229–244.

Telfer, E. S., and G. W. Scotter. 1975. Potential for game ranching in boreal aspen forests of western Canada. Journal of Range Management 28:172–180.

VerCauteren, K. C., P. W. Burke, G. E. Phillips, J. W. Fischer, N. W. Seward, B. A. Wunder, and M. J. Lavelle. 2007. Elk use of wallows and potential chronic wasting disease transmission. Journal of Wildlife Diseases 43:784–788.

Wallmo, O. C., L. H. Carpenter, W.L. Regelin, R. B. Gill, D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122–127.

Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. Annual Review of Ecological Systems 9:157–188.

Westfall, J. A., and L. R. Irby. 1993. A forage allocation model for four ungulate species in Theodore Roosevelt National Park. Final Report to the National Park Service.

Woeck, B. N. 2003. Demographics and space use of mule deer and white-tailed deer in Custer State Park, South Dakota. Thesis, University of Missouri, Columbia, Missouri, USA.

Table 1. Area (km^2) and intensity of habitat overlap among ungulates that have a Schoener's (1968) dietary overlap index > 0.50 in Custer State Park, SD, based on data collected 1993–2008.

Use	Species 1	Use	Species 2	Spring	Summer	Fall	Winter
High	Bison	High	Elk	9.36	9.10	23.90	18.32
High	Bison	Mid	Elk	17.49	18.56	7.33	6.15
Mid	Bison	High	Elk	33.92	33.54	29.08	28.35
Mid	Bison	Mid	Elk	34.09	32.89	11.11	9.52
High	Mule deer	High	Pronghorn	23.67	21.02		9.26
High	Mule deer	Mid	Pronghorn	28.82	47.67		38.03
Mid	Mule deer	High	Pronghorn	20.04	30.40		8.89
Mid	Mule deer	Mid	Pronghorn	34.00	62.04		25.58
High	Mule deer	High	White-tailed deer	23.13		17.75	
High	Mule deer	Mid	White-tailed deer	25.80		36.79	
Mid	Mule deer	High	White-tailed deer	19.73		8.86	
Mid	Mule deer	Mid	White-tailed deer	16.72		23.82	

Table 1, Continued.

Use	Species 1	Use	Species 2	Spring	Summer	Fall	Winter
High	Elk	High	White-tailed deer	27.68	27.68	19.09	19.09
High	Elk	Mid	White-tailed deer	25.79	25.79	51.89	51.89
Mid	Elk	High	White-tailed deer	17.48	17.48	10.17	10.17
Mid	Elk	Mid	White-tailed deer	19.29	19.29	19.55	19.55
High	Pronghorn	High	White-tailed deer		9.16	5.42	
High	Pronghorn	Mid	White-tailed deer		10.37	8.28	
Mid	Pronghorn	High	White-tailed deer		32.86	11.07	
Mid	Pronghorn	Mid	White-tailed deer		31.53	15.71	
High	Elk	High	Pronghorn		23.51		
High	Elk	Mid	Pronghorn		78.45		
Mid	Elk	High	Pronghorn		24.68		
Mid	Elk	Mid	Pronghorn		61.45		

Table 2. Original and adjusted values of the proportion of forage production available to each ungulate species based on resource selection and habitat overlap between ungulates, based on data collected 1993–2008, that have an Schoener's (1968) diet overlap index > 0.50 in Custer State Park, SD.

				Unadjusted selection		Adjustment to selection		Final selection	
Use	Species 1	Use	Species 2	Species 1	Species 2	Species 1	Species 2	Species 1	Species 2
High	Bison	High	Elk	1.0	1.0	0.6	0.4	0.6	0.4
High	Bison	Mid	Elk	1.0	0.5	0.6	0.4	0.6	0.2
Mid	Bison	High	Elk	0.5	1.0	0.6	0.4	0.3	0.4
Mid	Bison	Mid	Elk	0.5	0.5	0.6	0.4	0.3	0.2
High	Mule deer	High	Pronghorn	1.0	1.0	0.5	0.5	0.5	0.5
High	Mule deer	Mid	Pronghorn	1.0	0.5	0.5	0.5	0.5	0.3
Mid	Mule deer	High	Pronghorn	0.5	1.0	0.5	0.5	0.3	0.5
Mid	Mule deer	Mid	Pronghorn	0.5	0.5	0.5	0.5	0.3	0.3

Table 2, Continued.

				Unadjusted selection		Adjustment to selection		Final selection	
Use	Species 1	Use	Species 2	Species 1	Species 2	Species 1	Species 2	Species 1	Species 2
High	Mule deer	High	White-tailed deer	1.0	1.0	0.5	0.5	0.5	0.5
High	Mule deer	Mid	White-tailed deer	1.0	0.5	0.5	0.5	0.5	0.3
Mid	Mule deer	High	White-tailed deer	0.5	1.0	0.5	0.5	0.3	0.5
Mid	Mule deer	Mid	White-tailed deer	0.5	0.5	0.5	0.5	0.3	0.3
High	Elk	High	White-tailed deer	1.0	1.0	0.6	0.4	0.6	0.4
High	Elk	Mid	White-tailed deer	1.0	0.5	0.6	0.4	0.6	0.2
Mid	Elk	High	White-tailed deer	0.5	1.0	0.6	0.4	0.3	0.4
Mid	Elk	Mid	White-tailed deer	0.5	0.5	0.6	0.4	0.3	0.2

Table 2, Continued.

				Unadjusted selection		Adjustment to selection		Final selection	
Use	Species 1	Use	Species 2	Species 1	Species 2	Species 1	Species 2	Species 1	Species 2
High	Pronghorn	High	White-tailed deer	1.0	1.0	0.5	0.5	0.5	0.5
High	Pronghorn	Mid	White-tailed deer	1.0	0.5	0.5	0.5	0.5	0.3
Mid	Pronghorn	High	White-tailed deer	0.5	1.0	0.5	0.5	0.3	0.5
Mid	Pronghorn	Mid	White-tailed deer	0.5	0.5	0.5	0.5	0.3	0.3
High	Elk	High	Pronghorn	1.0	1.0	0.5	0.5	0.5	0.5
High	Elk	Mid	Pronghorn	1.0	0.5	0.5	0.5	0.5	0.3
Mid	Elk	High	Pronghorn	0.5	1.0	0.5	0.5	0.3	0.5
Mid	Elk	Mid	Pronghorn	0.5	0.5	0.5	0.5	0.3	0.3

Table 3. Proportion of each range and woodland site available to each ungulate species in Custer State Park, SD, during the spring season (1 March – 31 May), based on data collected 1993–2008.

Range or woodland site	Bison	Elk	Pronghorn	Mule deer	White-tailed deer
Clayey	0.71	0.09	0.75	0.33	0.11
Cool Slope	0.24	0.34	0.16	0.22	0.20
Overflow	0.45	0.19	0.69	0.56	0.23
Rocky side slope	0.12	0.47	0.24	0.29	0.15
Savannah	0.21	0.31	0.53	0.32	0.10
Shallow	0.51	0.14	0.66	0.26	0.11
Shallow ridge	0.25	0.28	0.04	0.40	0.09
Silty	0.65	0.10	0.72	0.31	0.17
Silty footslope	0.04	0.42	0.34	0.01	0.14
Steep cool slope	0.26	0.34	0.20	0.40	0.22
Steep rocky side slope	0.04	0.67	0.50	0.30	0.10
Steep warm slope	0.30	0.45	0.43	0.44	0.14
Stony hills	0.59	0.17	0.82	0.27	0.11
Thin upland	0.89	0.03	0.80	0.13	0.39
Warm slope	0.27	0.30	0.11	0.40	0.13
Prairie Dog Colony	0.45	0.22	0.58	0.32	0.13

Table 4. Proportion of each range and woodland site available to each ungulate species in Custer State Park, SD, during the summer, (1 June – 31 August), based on data collected 1993–2008.

Range or woodland site	Bison	Elk	Pronghorn	Mule deer	White-tailed deer
Clayey	0.74	0.04	0.31	0.32	0.06
Cool slope	0.24	0.21	0.11	0.24	0.11
Overflow	0.45	0.11	0.17	0.44	0.13
Rocky side slope	0.12	0.29	0.13	0.32	0.09
Savannah	0.22	0.16	0.20	0.32	0.06
Shallow	0.54	0.07	0.28	0.32	0.06
Shallow ridge	0.22	0.19	0.14	0.27	0.05
Silty	0.68	0.05	0.31	0.30	0.09
Silty footslope	0.04	0.24	0.22	0.04	0.08
Steep cool slope	0.26	0.21	0.08	0.32	0.12
Steep rocky side slope	0.04	0.37	0.20	0.27	0.05
Steep warm slope	0.31	0.29	0.13	0.48	0.09
Stony hills	0.62	0.09	0.28	0.31	0.06
Thin upland	0.79	0.01	0.30	0.16	0.21
Warm slope	0.27	0.22	0.11	0.36	0.08
Prairie dog colony	0.47	0.08	0.20	0.32	0.06

Table 5. Proportion of each range and woodland site available to each ungulate species in Custer State Park, SD, during the fall (1 September –30 November), based on data collected 1993–2008.

Range or woodland site	Bison	Elk	Pronghorn	Mule deer	White-tailed deer
Clayey	0.34	0.19	0.46	0.51	0.07
Cool slope	0.04	0.75	0.25	0.27	0.07
Overflow	0.20	0.27	0.13	0.43	0.15
Rocky side slope	0.05	0.62	0.26	0.35	0.07
Savannah	0.45	0.33	0.46	0.47	0.09
Shallow	0.28	0.24	0.39	0.41	0.13
Shallow ridge	0.55	0.31	0.30	0.45	0.07
Silty	0.33	0.22	0.31	0.41	0.12
Silty footslope	0.00	0.39	0.32	0.02	0.11
Steep cool slope	0.45	0.42	0.34	0.51	0.03
Steep rocky side slope	0.01	0.75	0.47	0.45	0.04
Steep warm slope	0.10	0.78	0.49	0.59	0.08
Stony hills	0.59	0.23	0.49	0.57	0.07
Thin upland	0.57	0.09	0.01	0.12	0.22
Warm slope	0.39	0.29	0.27	0.40	0.10
Prairie dog colony	0.37	0.50	0.48	0.53	0.08

Table 6. Proportion of each range and woodland site available to each ungulate species in Custer State Park, SD, during the winter (1 December – 28 Feburary), based on data collected 1993–2008.

Range or woodland site	Bison	Elk	Pronghorn	Mule deer	White-tailed deer
Clayey	0.34	0.19	0.32	0.42	0.12
Cool slope	0.03	0.75	0.09	0.32	0.10
Overflow	0.23	0.28	0.29	0.45	0.27
Rocky side slope	0.05	0.64	0.13	0.40	0.12
Savannah	0.43	0.33	0.21	0.52	0.17
Shallow	0.35	0.22	0.27	0.42	0.24
Shallow ridge	0.26	0.36	0.03	0.57	0.11
Silty	0.33	0.22	0.34	0.36	0.21
Silty footslope	0.02	0.40	0.44	0.03	0.13
Steep cool slope	0.21	0.53	0.10	0.51	0.06
Steep rocky side slope	0.02	0.77	0.25	0.40	0.07
Steep warm slope	0.18	0.68	0.12	0.65	0.15
Stony hills	0.59	0.24	0.35	0.40	0.12
Thin upland	0.56	0.08	0.73	0.13	0.27
Warm slope	0.11	0.56	0.04	0.57	0.17
Prairie dog colony	0.31	0.52	0.12	0.51	0.15

Table 7. Weights, herd composition and daily intake rates used to estimate carrying capacity of mule deer in Custer State Park, SD.

Age	Sex	Body weight (Kg)				Herd (%)	Daily Intake (% body weight)
		Spring	Summer	Fall	Winter		
Adult	Male	59.6	60.0	60.0	59.6	23	2
Adult	Female	59.2	59.0	59.0	59.2	43	4
Yearling	Male	49.5	52.5	55.3	58.2	3	3
Yearling	Female	44.6	48.8	53.0	57.1	5	3
Juvenile	Male	9.1	20.3	31.6	42.7	13	3
Juvenile	Female	8.4	18.2	28.1	37.8	13	3

Table 8. Weights, herd composition and daily intake rates used to estimate carrying capacity of white-tailed deer in Custer State Park, SD.

Age	Sex	Body weight (Kg)				Herd (%)	Daily Intake (% body weight)
		Spring	Summer	Fall	Winter		
Adult	Male	53.1	53.1	53.1	53.1	25	2.1
Adult	Female	47.8	47.8	47.8	47.8	44	4.0
Yearling	Male	48.2	49.6	51.0	52.5	3	3.0
Yearling	Female	42.8	44.3	45.7	47.1	5	3.0
Juvenile	Male	9.0	20.3	31.7	42.8	12	3.3
Juvenile	Female	8.3	18.0	27.8	37.3	12	3.3

Table 9. Weights, herd composition and daily intake rates used to estimate carrying capacity of pronghorn in Custer State Park, SD.

Age	Sex	Body weight (Kg)				Herd (%)	Daily Intake (% body weight)
		Spring	Summer	Fall	Winter		
Adult	Male	54.0	54.0	54.0	54.0	17	1.9
Adult	Female	48.0	48.0	48.0	48.0	31	3.0
Yearling	Male	39.8	43.0	46.4	51.0	7	1.9
Yearling	Female	39.0	40.0	42.0	44.0	7	1.9
Juvenile	Male	8.1	18.3	28.3	38.3	19	3.0
Juvenile	Female	8.1	18.3	28.3	38.3	19	3.0

Table 10. Weights, herd composition and daily intake rates used to estimate carrying capacity of bison in Custer State Park, SD.

Age	Sex	Body weight (Kg)				Herd (%)	Daily Intake (% body weight)
		Spring	Summer	Fall	Winter		
Adult	Male	720	720	756	800	12	1.7
Adult	Female	423	423	444	470	53	2.7
Yearling	Male	300	270	300	300	6	1.7
Yearling	Female	263	240	285	263	8	1.7
Juvenile	Male	87	204	291	295	9	3.1
Juvenile	Female	77	180	257	261	13	3.1

Table 11. Weights, herd composition and daily intake rates used to estimate carrying capacity of elk in Custer State Park, SD.

Age	Sex	Body weight (Kg)				Herd (%)	Daily Intake (% body weight)
		Spring	Summer	Fall	Winter		
Adult	Male	284.4	316.0	316.0	316.0	27	2.1
Adult	Female	201.6	224.0	224.0	224.0	33	3.0
Yearling	Male	178.0	201.3	247.8	293.6	9	2.1
Yearling	Female	146.0	159.1	185.4	211.3	9	2.1
Juvenile	Male	51.8	126.3	135.0	135.0	11	2.7
Juvenile	Female	52.7	125.4	130.0	130.0	11	2.7

Table 12. Seasonal carrying capacity estimates for ungulate species in Custer State Park, SD, under 25, 35, and 50% allowable use of total forage production for an average year of growing season precipitation and length.

	Fall			Winter			Spring			Summer		
Species	25	35	50	25	35	50	25	35	50	25	35	50
Bison	659	919	919	644	902	1136	500	500	500	500	648	726
Elk	337	337	337	300	300	484	699	696	1450	212	300	300
Mule deer	100	240	367	584	1649	2399	100	132	260	100	135	375
White-tailed deer	157	175	175	795	795	795	100	100	157	100	135	180
Pronghorn	100	100	157	541	359	491	237	434	434	100	150	150
Total	1353	1771	1955	2864	4005	5305	1636	1862	2801	1012	1368	1731

Table 13. Seasonal carrying capacity estimates for each ungulate species in Custer State Park, SD, based on 100% allowable use of total forage production and model runs that incorporated habitat and diet overlap as well as resource selection of each species (A), did not incorporate resource selection but did incorporate diet overlap (B), and did not incorporate habitat overlap, diet overlap, or resource selection (C).

	Spring			Summer			Fall			Winter		
Species	A	B	C	A	B	C	A	B	C	A	B	C
Bison	794	500	2202	726	2000	2084	919	1901	1965	1136	2576	2576
Elk	1453	2901	3753	457	300	759	337	337	337	633	300	1303
Mule deer	260	100	899	777	881	1750	368	720	816	2399	4974	6036
White-tailed deer	244	100	1249	180	180	180	175	945	945	795	3483	6378
Pronghorn	434	2256	2691	150	867	1339	216	100	860	907	911	3304
Total	3185	5857	10794	2290	4228	6112	2015	4003	4923	5870	12244	19597

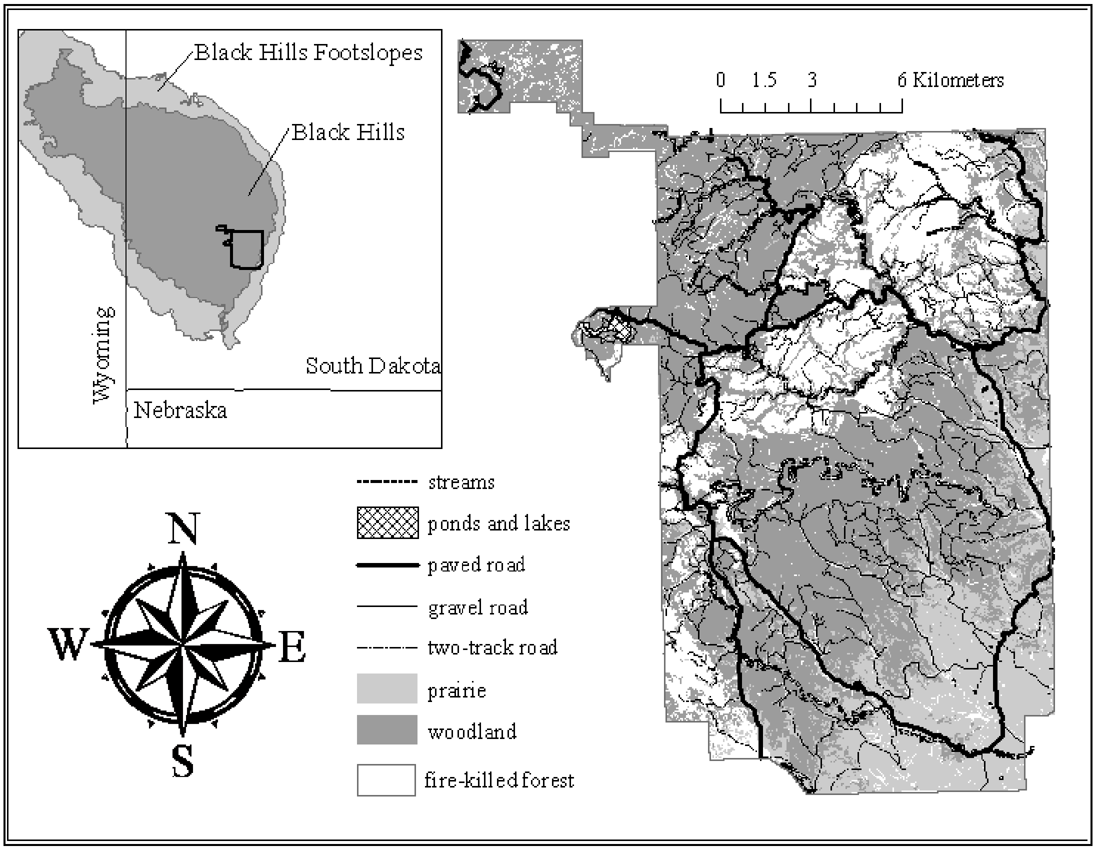

Figure 1. Major habitat types and features in Custer State Park, SD.

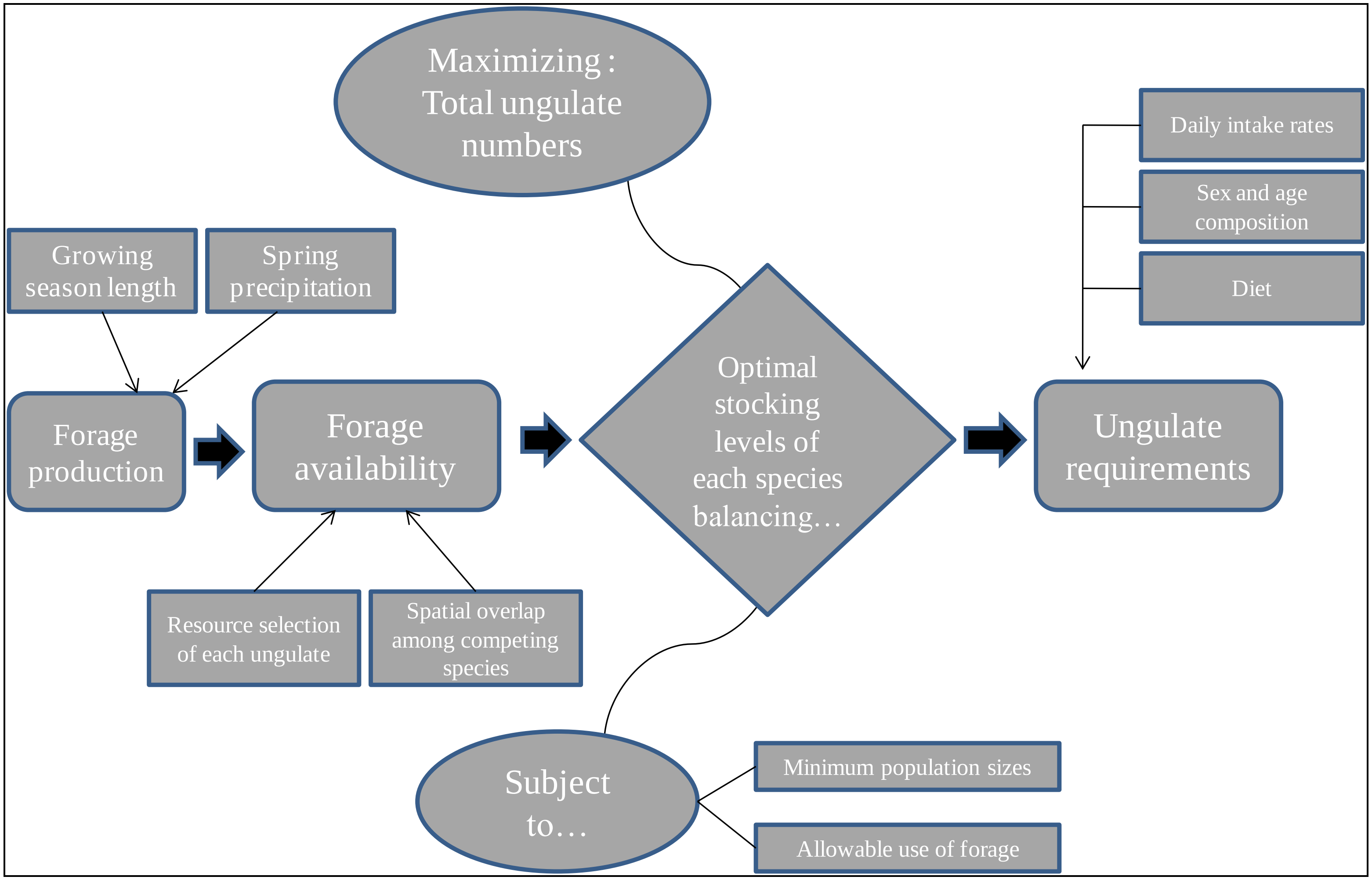

Figure 2. Optimal solution and constraints of linear optimization forage allocation model for Custer State Park, SD, adapted from Kuzyk et al. (2009).

APPENDIX I. LOCATION OF FORAGE EXCLUSION CAGES IN CUSTER STATE PARK, SOUTH DAKOTA

Point_ID	Range site	Easting	Northing
C_05_00	Clayey	632069.48	4835527.80
C_05_01	Clayey	632751.16	4838244.11
C_05_02	Clayey	631613.42	4834645.17
C_05_03	Clayey	632772.08	4833172.93
C_05_04	Clayey	633711.35	4846017.51
C_05_05	Clayey	633378.00	4833891.00
C_05_06	Clayey	633333.66	4839955.59
C_05_07	Clayey	632426.39	4843804.59
C_05_08	Clayey	630590.94	4835655.85
C_05_09	Clayey	630031.92	4833426.57
CS_06_00	cool slope	631388.15	4847719.73
CS_06_01	cool slope	631665.42	4848024.59
CS_06_02	cool slope	630860.32	4849050.35
CS_06_14	cool slope	632647.00	4841859.00
CS_06_19	cool slope	633169.00	4844964.00
CS_06_24	cool slope	631333.00	4847119.00
CS_06_30	cool slope	630859.00	4849386.00
CS_06_33	cool slope	631929.00	4849865.00
CS_06_35	cool slope	632960.00	4850931.00
O_05_00	Overflow	625048.72	4842605.94
O_05_02	Overflow	623749.38	4841437.42
O_05_03	Overflow	626933.55	4847829.32
O_05_04	Overflow	623522.38	4841686.56
O_05_05	Overflow	619088.02	4845876.73
O_05_06	Overflow	623308.29	4837763.46
O_05_07	Overflow	630255.68	4838643.75
O_05_08	Overflow	624001.00	4838751.59
O_05_09	Overflow	625282.95	4850821.92
O_06_01	Overflow	621271.00	4841574.00
O_06_02	Overflow	623960.00	4836952.00
O_08_01	Overflow	624266.00	4832477.00
O_08_02	Overflow	624320.00	4833674.00
O_08_03	Overflow	624461.00	4833526.00
O_08_04	Overflow	624608.00	4833068.00
O_08_05	Overflow	624883.00	4841270.00
O_08_06	Overflow	625309.00	4832516.00

Point_ID	Range site	Easting	Northing
RSS_05_00	rocky side slope	627447.62	4840849.51
RSS_05_01	rocky side slope	624279.83	4839265.15
RSS_05_02	rocky side slope	622773.70	4840924.48
RSS_05_03	rocky side slope	629370.90	4844348.95
RSS_05_04	rocky side slope	628072.53	4838381.38
RSS_05_05	rocky side slope	631802.11	4852349.88
RSS_05_06	rocky side slope	621570.48	4845145.56
RSS_05_07	rocky side slope	625545.39	4840376.38
RSS_05_08	rocky side slope	620958.92	4851931.57
RSS_05_09	rocky side slope	622246.85	4848830.47
RSS_06_00	rocky side slope	627715.51	4836718.74
RSS_06_01	rocky side slope	623914.13	4836338.09
RSS_06_02	rocky side slope	626061.11	4837568.02
RSS_06_03	rocky side slope	623721.35	4839758.81
RSS_06_04	rocky side slope	614524.00	4856057.82
RSS_06_05	rocky side slope	630391.25	4851672.53
RSS_06_06	rocky side slope	623443.69	4835742.07
RSS_06_07	rocky side slope	621191.79	4847031.79
RSS_06_08	rocky side slope	625886.51	4837253.38
RSS_06_09	rocky side slope	622362.22	4835451.66
RSS_06_10	rocky side slope	628435.23	4851230.63
RSS_06_11	rocky side slope	629542.78	4845303.48
RSS_06_12	rocky side slope	626506.63	4835330.36
RSS_06_13	rocky side slope	627873.54	4839252.25
RSS_06_14	rocky side slope	622440.93	4837753.57
RSS_06_15	rocky side slope	623762.49	4841025.16
RSS_06_16	rocky side slope	625385.02	4851335.06
RSS_06_17	rocky side slope	624925.57	4834501.87
RSS_06_18	rocky side slope	621377.35	4852515.23
RSS_06_19	rocky side slope	621269.84	4849807.39
RSS_06_20	rocky side slope	622606.54	4847323.50
RSS_06_21	rocky side slope	621407.69	4847678.32
RSS_06_22	rocky side slope	624587.52	4844899.87
RSS_06_23	rocky side slope	625775.43	4847171.52
RSS_06_24	rocky side slope	629811.57	4848105.10
RSS_06_25	rocky side slope	627388.35	4844006.05

Point_ID	Range site	Easting	Northing
RSS_06_26	rocky side slope	625387.00	4834939.15
RSS_06_27	rocky side slope	624964.03	4834560.72
RSS_06_28	rocky side slope	625161.38	4840720.81
RSS_06_29	rocky side slope	623206.86	4846311.07
RSS_06_30	rocky side slope	622605.38	4836574.26
RSS_06_31	rocky side slope	626091.00	4839635.00
RSS_08_01	rocky side slope	620053.00	4847114.00
RSS_08_02	rocky side slope	626063.00	4844424.00
SA_05_00	Savannah	622792.50	4833634.15
SA_05_01	Savannah	625243.89	4834365.93
SA_05_02	Savannah	627346.45	4835938.29
SA_05_03	Savannah	622769.04	4834266.74
SA_05_04	Savannah	623813.18	4833361.59
SA_05_05	Savannah	630566.63	4849199.10
SA_05_06	Savannah	623877.68	4833710.02
SA_05_07	Savannah	623256.69	4832991.88
SA_05_08	Savannah	623747.46	4833892.16
SA_05_09	Savannah	625427.25	4832487.71
SA_08_02	Savannah	622784.00	4833419.00
SA_08_03	Savannah	623217.00	4833644.00
SA_08_04	Savannah	623288.00	4833706.00
SA_08_05	Savannah	623384.00	4833684.00
SA_08_06	Savannah	623721.00	4833650.00
SCS_05_00	steep cool slope	631885.61	4847318.01
SCS_05_01	steep cool slope	631545.77	4847434.78
SCS_05_02	steep cool slope	632607.40	4848619.53
SCS_05_03	steep cool slope	630864.70	4838737.84
SCS_05_04	steep cool slope	631933.10	4849584.28
SCS_05_05	steep cool slope	632777.11	4847024.09
SCS_05_06	steep cool slope	631123.56	4846561.15
SCS_05_07	steep cool slope	632245.17	4847988.02
SCS_05_08	steep cool slope	632591.93	4848299.51
SCS_05_09	steep cool slope	631885.63	4848184.61
SCS_06_00	steep cool slope	628579.92	4835589.62
SCS_06_01	steep cool slope	631362.75	4847931.02
SCS_06_02	steep cool slope	631090.04	4839617.90

Point_ID	Range site	Easting	Northing
SCS_06_03	steep cool slope	631338.49	4847936.37
SCS_06_04	steep cool slope	631898.81	4848959.07
SCS_06_05	steep cool slope	631898.39	4847734.91
SCS_06_06	steep cool slope	631624.45	4847349.01
SCS_06_26	steep cool slope	631849.00	4850931.00
SCS_06_28	steep cool slope	631898.00	4849039.00
SF_05_00	silty footslope	621346.77	4845357.13
SF_05_01	silty footslope	627028.21	4840021.67
SF_05_02	silty footslope	627030.65	4840214.63
SF_05_03	silty footslope	621076.72	4845876.11
SF_05_04	silty footslope	621060.26	4845896.34
SF_05_05	silty footslope	621089.49	4845762.44
SF_05_06	silty footslope	628850.24	4853084.59
SF_05_07	silty footslope	627604.30	4852700.99
SF_05_08	silty footslope	626476.94	4840244.99
SF_05_09	silty footslope	621313.29	4839617.55
SH_05_00	Shallow	632900.60	4836986.47
SH_05_01	Shallow	626237.52	4832593.05
SH_05_02	Shallow	633674.25	4846045.53
SH_05_03	Shallow	631809.84	4838207.40
SH_05_04	Shallow	633189.07	4843232.03
SH_05_05	Shallow	628111.51	4834590.27
SH_05_06	Shallow	626393.09	4832686.89
SH_05_07	Shallow	629125.51	4835176.11
SH_05_08	Shallow	632214.65	4845704.59
SH_05_09	Shallow	632910.97	4836392.21
SH_08_01	Shallow	625588.00	4832697.00
SH_08_02	Shallow	628792.00	4836906.00
SH_08_03	Shallow	631586.00	4832786.00
SH_08_04	Shallow	633522.00	4845652.00
SH_08_05	Shallow	633628.00	4845934.00
SHR_05_00	shallow ridge	631697.28	4833735.86
SHR_05_01	shallow ridge	625798.59	4832920.69
SHR_05_02	shallow ridge	632600.49	4832272.29
SHR_05_03	shallow ridge	631758.68	4849023.44
SHR_05_04	shallow ridge	628031.89	4835284.93

Point_ID	Range site	Easting	Northing
SHR_05_05	shallow ridge	627531.17	4835474.18
SHR_05_06	shallow ridge	627124.64	4832691.11
SHR_05_07	shallow ridge	631450.53	4849388.68
SHR_05_08	shallow ridge	633162.47	4843445.22
SHR_05_09	shallow ridge	631367.50	4848316.49
SHR_06_00	shallow ridge	633400.23	4836161.63
SHR_06_01	shallow ridge	627559.91	4832155.86
SHR_06_02	shallow ridge	627446.59	4832655.62
SHR_06_03	shallow ridge	631265.24	4848672.35
SHR_06_04	shallow ridge	631582.33	4848871.30
SHR_06_05	shallow ridge	633624.82	4843608.07
SHR_06_06	shallow ridge	627127.85	4833214.31
SHR_06_07	shallow ridge	630705.86	4834513.20
SI_05_00	Silty	630061.59	4837601.39
SI_05_01	Silty	626951.91	4839150.08
SI_05_02	Silty	622103.04	4840499.74
SI_05_03	Silty	629745.69	4838636.18
SI_05_04	Silty	627257.52	4834452.88
SI_05_05	Silty	631746.33	4845279.51
SI_05_06	Silty	632964.85	4833647.80
SI_05_07	Silty	628220.77	4836709.49
SI_05_08	Silty	626187.26	4834094.55
SI_05_09	Silty	627327.71	4833091.63
SI_05_10	Silty	627174.65	4834538.37
SI_06_00	Silty	627764.67	4838889.54
SI_06_01	Silty	627546.47	4832924.49
SI_08_01	Silty	623058.00	4833204.00
SI_08_02	Silty	623078.00	4833449.00
SI_08_03	Silty	623502.00	4833417.00
SI_08_03	Silty	623747.00	4833114.00
SI_08_04	Silty	626193.00	4851276.00
SI_08_05	Silty	629762.00	4837981.00
SI_08_06	Silty	630194.00	4834887.00
SI_08_07	Silty	632775.00	4843421.00
SI_08_08	Silty	633169.00	4841340.00
SI_08_09	Silty	633759.00	4840670.00

Point_ID	Range site	Easting	Northing
SRSS_05_00	steep rocky side slope	631129.67	4852360.14
SRSS_05_01	steep rocky side slope	623955.55	4845384.54
SRSS_05_02	steep rocky side slope	616645.60	4855442.48
SRSS_05_03	steep rocky side slope	627173.85	4842507.22
SRSS_05_04	steep rocky side slope	618188.03	4855922.19
SRSS_05_05	steep rocky side slope	621347.17	4844235.54
SRSS_05_06	steep rocky side slope	621258.17	4842701.57
SRSS_05_07	steep rocky side slope	628107.17	4846766.60
SRSS_05_08	steep rocky side slope	631475.51	4851550.65
SRSS_05_09	steep rocky side slope	623836.59	4837413.26
SRSS_06_00	steep rocky side slope	623715.30	4841589.84
SRSS_06_01	steep rocky side slope	622126.39	4842636.69
SRSS_06_02	steep rocky side slope	626991.19	4846098.75
SRSS_06_03	steep rocky side slope	622817.67	4845213.45
SRSS_06_03	steep rocky side slope	622814.00	4844791.00
SRSS_06_04	steep rocky side slope	625001.36	4850187.80
SRSS_06_05	steep rocky side slope	625446.03	4838097.97
SRSS_06_06	steep rocky side slope	626777.49	4841376.24
SRSS_06_07	steep rocky side slope	621400.51	4852169.04
SRSS_06_08	steep rocky side slope	630919.01	4850574.56
SRSS_06_09	steep rocky side slope	629629.55	4853205.97
SRSS_06_10	steep rocky side slope	622139.27	4834986.01
SRSS_06_11	steep rocky side slope	628862.24	4851104.27
SRSS_06_12	steep rocky side slope	626037.76	4848771.29
SRSS_06_14	steep rocky side slope	626964.16	4845593.62
SRSS_06_15	steep rocky side slope	621730.39	4843571.68
SRSS_06_16	steep rocky side slope	626771.98	4843192.92
SRSS_06_17	steep rocky side slope	626206.93	4843481.73
SRSS_06_18	steep rocky side slope	626045.24	4843612.96
SRSS_06_19	steep rocky side slope	628926.04	4838203.29
SRSS_06_20	steep rocky side slope	622615.00	4843945.00
SRSS_08_01	steep rocky side slope	627591.00	4852757.00
STH_05_00	stony hills	628443.10	4833302.91
STH_05_01	stony hills	631562.45	4836386.38
STH_05_02	stony hills	632392.50	4836743.73
STH_05_03	stony hills	627952.16	4832139.67

Point_ID	Range site	Easting	Northing
STH_05_04	stony hills	629942.28	4838984.82
STH_05_05	stony hills	631297.52	4835396.71
STH_05_06	stony hills	633442.86	4837722.35
STH_05_07	stony hills	633525.43	4849392.37
STH_05_08	stony hills	630351.68	4836955.30
STH_05_09	stony hills	628803.47	4834896.58
STH_06_00	stony hills	631780.00	4843167.54
STH_06_01	stony hills	633391.99	4850557.67
STH_06_02	stony hills	631989.66	4834463.91
STH_06_03	stony hills	628907.50	4834784.83
STH_06_04	stony hills	631742.23	4840470.30
STH_06_05	stony hills	633086.30	4837512.41
STH_06_06	stony hills	631778.41	4843244.95
STH_06_07	stony hills	632606.68	4837876.25
STH_06_08	stony hills	628052.01	4832486.61
STH_06_09	stony hills	632603.65	4836920.63
STH_06_10	stony hills	632234.14	4852533.29
STH_06_11	stony hills	632095.09	4846588.81
STH_06_12	stony hills	633245.73	4845516.73
STH_06_13	stony hills	633551.29	4834552.63
STH_06_14	stony hills	633711.08	4846316.34
STH_06_15	stony hills	632736.66	4836752.51
STH_06_16	stony hills	629036.91	4832034.16
STH_06_17	stony hills	631962.82	4844005.71
STH_06_18	stony hills	621375.02	4840366.02
STH_06_19	stony hills	632449.72	4844050.40
STH_06_20	stony hills	630215.36	4836988.20
STH_06_21	stony hills	625067.51	4837206.76
STH_06_22	stony hills	628972.03	4832230.02
STH_06_23	stony hills	632701.56	4833118.77
STH_06_24	stony hills	630501.56	4836176.08
STH_06_25	stony hills	628426.01	4832778.74
STH_06_26	stony hills	630053.15	4837944.69
STH_06_27	stony hills	628921.13	4833483.29

Point_ID	Range site	Easting	Northing
STH_06_28	stony hills	631115.36	4831895.71
STH_06_29	stony hills	631783.42	4832477.55
STH_06_30	stony hills	622439.08	4839487.89
STH_06_31	stony hills	630080.33	4837764.09
STH_06_32	stony hills	630072.39	4840485.20
STH_06_33	stony hills	624840.06	4837867.45
STH_06_34	stony hills	632135.44	4853106.13
STH_06_35	stony hills	633790.56	4834333.44
STH_06_36	stony hills	632864.34	4834256.03
STH_06_37	stony hills	632254.10	4853256.22
STH_06_38	stony hills	622489.98	4839168.26
STH_06_39	stony hills	629412.35	4833826.13
STH_06_40	stony hills	632972.32	4838152.13
STH_06_41	stony hills	633377.86	4850143.89
STH_06_42	stony hills	632678.28	4831793.79
STH_06_43	stony hills	632210.89	4840471.50
STH_06_44	stony hills	627733.80	4832399.48
STH_06_45	stony hills	633453.33	4851130.79
STH_06_46	stony hills	623457.94	4838390.10
STH_06_47	stony hills	623520.58	4838677.84
STH_06_48	stony hills	628701.49	4834796.22
STH_06_49	stony hills	632845.93	4840353.69
STH_08_01	stony hills	622932.00	4838657.00
STH_08_02	stony hills	623447.00	4838726.00
STH_08_03	stony hills	623974.00	4833856.00
STH_08_04	stony hills	624004.00	4833713.00
STH_08_05	stony hills	624133.00	4833133.00
STH_08_06	stony hills	624816.00	4832889.00
STH_08_07	stony hills	624841.00	4832947.00
STH_08_08	stony hills	632427.00	4842821.00
STH_08_10	stony hills	633195.00	4837500.00
SWS_05_00	steep warm slope	632362.25	4839850.56
SWS_05_01	steep warm slope	629682.59	4842371.29
SWS_05_02	steep warm slope	633609.90	4839320.99
SWS_05_03	steep warm slope	631577.21	4850984.85
SWS_05_04	steep warm slope	631536.23	4841497.73

Point_ID	Range site	Easting	Northing
SWS_05_05	steep warm slope	631699.89	4850247.93
SWS_05_06	steep warm slope	631778.04	4840910.61
SWS_05_07	steep warm slope	632811.85	4848179.34
SWS_05_08	steep warm slope	633656.14	4846712.90
SWS_05_09	steep warm slope	630215.83	4841882.11
SWS_08_01	steep warm slope	631885.00	4850749.00
SWS_08_01	steep warm slope	630548.00	4833308.00
SWS_08_02	steep warm slope	631870.00	4838511.00
TU_05_00	thin upland	631022.65	4843704.76
TU_05_01	thin upland	631227.95	4843684.45
TU_05_02	thin upland	631430.04	4843468.06
TU_05_03	thin upland	630900.53	4843727.52
TU_05_04	thin upland	631037.74	4843636.11
TU_05_05	thin upland	631276.01	4843474.05
TU_05_06	thin upland	631198.80	4843555.23
TU_05_07	thin upland	630992.34	4843748.48
TU_05_08	thin upland	631050.84	4843630.43
TU_05_09	thin upland	630851.33	4843871.20
WS_05_00	warm slope	630422.86	4844642.77
WS_05_01	warm slope	631312.47	4840185.97
WS_05_02	warm slope	631195.69	4845543.61
WS_05_03	warm slope	631158.60	4845419.01
WS_05_04	warm slope	631444.56	4839427.16
WS_05_05	warm slope	631012.58	4839774.28
WS_05_06	warm slope	632926.84	4843771.40
WS_05_07	warm slope	630553.67	4839449.81
WS_05_08	warm slope	632049.54	4839245.82
WS_05_09	warm slope	630628.65	4844638.17
WS_06_00	warm slope	632191.97	4837586.83
WS_06_01	warm slope	626365.81	4833277.14
WS_06_02	warm slope	631316.07	4844691.73
WS_06_03	warm slope	628767.44	4836667.06
WS_06_04	warm slope	628657.80	4835824.04
WS_06_05	warm slope	633487.47	4845734.07
WS_06_06	warm slope	630457.55	4845338.71
WS_06_07	warm slope	630474.75	4839700.32

Point_ID	Range site	Easting	Northing
WS_06_08	warm slope	630467.01	4840142.30
WS_06_09	warm slope	633051.72	4841462.30
WS_06_10	warm slope	630262.77	4844983.91
WS_06_11	warm slope	632411.50	4846670.59
WS_06_12	warm slope	630916.56	4845020.25
WS_06_13	warm slope	627702.25	4834887.73
WS_06_14	warm slope	632932.01	4841456.00
WS_06_15	warm slope	631090.47	4840155.71
WS_06_16	warm slope	630516.70	4839992.95
WS_06_17	warm slope	628990.23	4838642.74
WS_06_18	warm slope	631794.01	4839204.08
WS_06_19	warm slope	629402.74	4836081.72
WS_06_20	warm slope	630409.39	4846008.86

APPENDIX II. RESOURCE SELECTION MODELS USED FOR UNGULATE SPECIES IN CSP.

Mule Deer: logit(p)summer = 4.106 – 0.001(elevation) – 0.837(visibility from secondary road) + 0.0002(tree density) – 0.068(water) – 0.028(edge density) – 0.0002(distance to primary road) – 0.0001(distance to secondary road) – 7.8E-07(distance to primary road×tree density)

logit(p)winter = 0.887 + 0.068(slope) – 0.968(visibility from primary road) + 0.0002(distance to primary road) +0.049(edge density) – 0.08(water) + 0.142(distance to tertiary roads) – 4.9E-05(distance to primary roads × slope)

White-tailed Deer: logit(p)summer = 6.621 – 0.002(elevation) + 0.0006(tree density) – 0.0002(distance to secondary road) – 0.538(visibility from tertiary road) – 0.518(visibility from secondary road) + 0.411(visibility from primary road) – 0.083(edge density) – 0.057(water) – 0.266(distance to tertiary roads)

logit(p)winter = 4.747 – 0.013(slope) – 0.002(elevation) – 0.0002(distance to secondary road) + 0.0006(distance to primary road) – 0.728(visibility from tertiary road) – 0.356(visibility from secondary road) – 0.422(visibility from primary road) – 0.052(water) – 0.073(edge density) – 1.7E-05(distance to primary road×slope)

Elk: logit(p)summer = -0.478 – 0.303(visibility from tertiary road) + 0.046(slope) – 0.001(edge) + 0.0013(tree density) + 0.0004(distance to secondary road) + 0.183(aspect) – 0.014(distance to tertiary road) – 3.9E-07(distance to secondary road × tree density) – 3.6E-05(distance to tertiary road ×slope) – 8.2E-06(distance to secondary road ×slope)

logit(p)winter = 2.939 – 0.249(visibility from tertiary road) – 0.23(visibility from secondary road) – 0.04(edge) + 0.002(distance to secondary road) – 0.001(elevation) + 0.002(tree density) – 0.031(distance to tertiary road) – 4.1E-07(distance to secondary road× tree density)

VITA

Barbara Jean Keller was born in Grand Prairie, Texas, on May 8, 1980. She attended and graduated from Fossil Ridge High School, located in Keller, Texas, in 1998. Barbara attended Northland College, in Ashland, Wisconsin, from 1998 to 2002. She earned a Bachelor of Science degree in Natural Resource Management from Northland College in May 2002. While at Northland, she participated in the Ronald E. McNair Scholars program. Her senior thesis was entitled "Habitat use of Southern flying squirrels (*Glaucomys volans*) in Northern Wisconsin".

After receiving her BS, Barbara was accepted into graduate school at New Mexico State University. She worked with Dr. Louis C. Bender at the USGS Cooperative Fish and Wildlife Research Unit studying the impacts of road-related disturbance on a bighorn sheep population in Rocky Mountain National Park, Colorado. She earned her Master of Science degree from NMSU in July of 2005. Shortly before earning her MS, Barbara was accepted into a PhD program at the University of Missouri-Columbia. Her work with Dr. Joshua Millspaugh at MU centered on achieving a greater understanding of the spatial and temporal use of resources by an ungulate assemblage in Custer State Park, South Dakota.

Barbara has served as primary and co-author on 5 peer-reviewed publications and book chapters. She has presented research findings at 6 conferences and research forums, and won awards at two of those events. Barbara has collaborated with numerous state and federal agencies throughout her career including the National Park Service, USGS, South Dakota Game, Fish and Parks department, and the Missouri Department of Conservation.

Barbara currently works as a post-doctoral research scientist for MU and the Missouri Department of Conservation. She is evaluating resource selection, population dynamics, and other factors affecting a reintroduced elk population in Missouri. Barbara hopes to continue working with ungulates throughout her career, producing research that facilitates the conservation and management of these unique species.