Public Abstract
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Graduation Term:SS 2011
Department:Fisheries & Wildlife
Degree:PhD
Title:FACTORS AFFECTING SPATIAL AND TEMPORAL DYNAMICS OF AN UNGULATE ASSEMBLAGE IN THE BLACK HILLS, SOUTH DAKOTA

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 82â€“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 which pool locations across individuals will likely miss the full suite of factors affecting resource selection of ungulates, including gregarious species which form large groups.

We used microhistological techniques to estimate diet composition of each ungulate species, and calculated Schoenerâ€™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 500â€“659 bison, 212â€“699 elk, 100â€“584 mule deer, 100â€“795 white-tailed deer, and 100 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 which 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 which 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.