FINAL RESEARCH REPORT

JARBIDGE ELK HERD HABITAT EVALUATION:

NEVADA DEPARTMENT OF WILDLIFE HUNT UNIT O72

By

Jeffrey L. Beck, Ph.D.

James M. Peek, Ph.D.

Department of Fish and Wildlife Resources

University of Idaho

Moscow, Idaho 83844

January 2004

STUDY SUPPORTERS

Cover photo of elk in the East Fork of the Jarbidge River drainage provided by Merlin McColm, Elko, Nevada. Photo from an original oil painting by Brent Todd, Salt Lake City, Utah.

Suggested Citation:

Beck, J. L., and J. M. Peek. 2004. Jarbidge elk herd habitat evaluation: Nevada Department of Wildlife hunt unit 072. Final research report. Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho, USA. 172 pp.

ABSTRACT

Our primary research objective was to develop an elk carrying capacity model to estimate population levels that would not impair rangeland productivity in the Jarbidge Mountains of northeastern Nevada. Fieldwork was critical to obtain baseline data for model parameters such as habitat use and availability, diet composition, and forage nutrient abundance. Ninety-three elk were translocated into the Jarbidge Mountains in the 1990s; this population exhibited high growth rates and is predicted to increase to 1,110 by 2008.

We evaluated production, species richness, and use of herbage standing crop in and outside exclosures across 3 seasons to better understand the effects of grazing by cattle and elk on mountain meadows in northeastern Nevada. Forbs declined throughout summer and total use clipping treatments in early and mid-summer resulted in low regrowth of forbs.

We determined cattle, domestic sheep, elk, and mule deer diets with microhistological fecal analysis. Summer elk diets were largely composed of forbs. Diet group means did not differ between elk in spring with sheep in summer, elk in summer with deer and sheep, and cattle with sheep in summer. Twelve common forage species formed 44.2 to 85.3% of elk, deer, cattle, and sheep diets.

We estimated crude protein (CP), digestible energy (DE) and macrominerals in 12 common forage species to assess whether nutrient levels met summer seasonal lactating cow elk requirements. Crude protein and DE decreased in herbs and woody browse across summer seasons and CP in lupines and snowbrush ceanothus provided reliably high levels of CP across all seasons. The most limiting nutrient to lactating cows was DE.

Logistic regression modeling provided strong evidence in support of water and forage availability influencing elk habitat selection. We incorporated regression coefficients into resource selection functions (RSFs), or probabilities proportional to elk habitat use. We used RSFs to redistribute economic nutritional carrying capacity (I_{NCC}) estimates at 2 energetic performance levels for 236-kg lactating cow elk in autumn 1999 and 2000 over the summer range and then accordingly readjusted I_{NCC} estimates. Unadjusted I_{NCC} estimates predicted elk use of aspen and sagebrush–herb communities above nutritional resources at both performance levels in both years.

ACKNOWLEDGEMENTS

We thank field technicians Jake Bieker, Jesse Lewis, Lara Peterson, Carl Rudeen, and Kate Smolski for their hard work, insights, and assistance in data collection. Don Klebenow, Bob McGinty, and Don Noorda were capable volunteers. Don King, a retired U.S. Fish and Wildlife Service fisheries biologist whose work toward restoring abundant populations of elk to Nevada ranges was an inspiration. Don went out of his way to ensure many aspects of the project in Nevada were organized and ran smoothly. Eva Strand, College of Natural Resources GIS and Remote Sensing Lab, University of Idaho, provided exceptional help with geographic analyses and software. We thank Dale Everson, Oz Garton, Ken Newman, Kirk Steinhorst, and Chris Williams, all University of Idaho, for their help with quantitative questions. Several graduate students provided helpful statistical explanations including Ann Abbott, Jeff Manning, and Deb Montgomery. Karen Launchbaugh, University of Idaho, and Bruce Davitt, Washington State University, provided use of their lab facilities for nutritional analyses. John Cook, National Council for Air and Stream Improvement, Incorporated, offered many insights on elk nutritional ecology. Mark Boyce, University of Alberta, provided helpful comments on habitat modeling. Steve Brunsfeld, College of Natural Resources Herbarium, University of Idaho, verified plant voucher specimens. Elsie Watson provided a thorough proofread. Karla Makus, Linda Kisha, and Delaine Hawley of the Department of Fish and Wildlife Resources, University of Idaho, were particularly helpful with clerical needs.

Forest Service employees Dave Aicher, Will Amy, Fred Frampton, Jay Frederick, Cathy Jean, Teri Haney, Cheri Howell, Mike McNeil, Dave Prevedel, John Speck, and Bonnie Whalen; Nevada Division of Wildlife employees Larry Barngrover, Larry Gilbertson, and Joe Williams; and Bureau of Land Management employees Jim Klott, Ray Lister, and Ken Undlin all provided assistance at various times during our study. It was our privilege to interact with the insightful and supportive ranchers from the 71 Livestock Association, including Bert Brackett, Chet Brackett, Ira Brackett, Jarod Brackett, Marc Brackett, Kevin Chapin, Maurice Guerry, Mike Guerry, Charlie Liesen, and Randall Brewer. USDA Humboldt-Toiyabe National Forest, Nevada Division of Wildlife (now Nevada Department of Wildlife), USDI Bureau of Land Management, Rocky Mountain Elk Foundation, National Fish and Wildlife Foundation, Nevada Bighorns Unlimited, Elko Bighorns Unlimited, Safari Club International, the Cooperative Fish and Wildlife Research Unit, and the College of Natural Resources, University of Idaho supported our research.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

APPENDIX 1

APPENDIX 2

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 5

APPENDIX 1

APPENDIX 2

EXECUTIVE SUMMARY

Chapter 1

Elk Population Characteristics, Nevada Division of Wildlife Hunt Unit 072, 1990–2003

Abstract

Elk (*Cervus elaphus*) are native to northeastern Nevada, but were extirpated by the early 1900s. An agreement between 5 natural resource agencies and the 71 Livestock Association led to the reintroduction of 93 elk from Colorado, Oregon, and Utah into Nevada Division of Wildlife Hunt Unit 072 in winters 1990, 1991, and 1995. Elk reached an initial population objective of 300 by 1996 and were maintained near this level through antlerless sport harvest until 1999. Nevada Division of Wildlife minimum population estimates indicated the population increased to 555 individuals in 2003 after substantial antlerless harvests ended in 1998. Geometric mean finite rate of increase was $\lambda = 1.08$ during the period of antlerless elk hunting (1995–1999) and increased to $\lambda = 1.15$ following release from hunting (2000–2003). In the absence of substantial cow harvests, this population is predicted to double to 1,110 animals in 5 years and to triple to 1,650 animals in about 8 years with current growth rates. Calves to 100 cow ratios and bulls to 100 cow ratios in summer and winter indicate this population was very productive and contained a high ratio of bulls per 100 cows. Hunters harvested 118 of 463 (25.5%) antlerless elk permits issued from 1995 to 1999. Harvest success for bull elk from 1994 to 2002 was 95 for 124 permits, or 76.6%.

Objective

1) Provide an analysis and synthesis of population information for elk reintroduced into the Jarbidge Mountains of northeastern Nevada in the 1990s.

Findings and Implications

1) High ratios of calves to cows and bulls to cows indicate this elk population provides optimal hunting opportunities.
2) Growth rates indicate this population is rapidly expanding and is predicted to reach or surpass Nevada Division of Wildlife population objectives of 1,000 ± 100 by 2008.
3) Aggressive antlerless harvest strategies were effective in slowing population growth rates.

Chapter 2

Herbage Productivity and Ungulate Use of Northeastern Nevada Mountain Meadows

Abstract

The effects of grazing by cattle and elk on mountain meadows in northeastern Nevada are poorly understood. We evaluated production, species richness, and use of herbage standing crop in and outside 3 meadow exclosures in northeastern Nevada's Jarbidge Mountains across 3 seasons in 1999 and 2000. Treatments included exclusion of all grazers (control), exclusion of cattle, but not wildlife (wildlife treatment), and combined cattle and wildlife grazing (cattle treatment). The combined cattle and wildlife use treatment was designated the cattle treatment because most use was attributable to cattle. There was less forb biomass in fall than in early or mid-summer, but no difference in forb standing crop from early to mid-summer across all treatments. There were no differences in graminoid standing crop among treatments in 1999, while there was significantly less graminoid crop in cattle treatments in 2000 than in the control or wildlife treatments. Species lists in exclosures and cattle treatments overlapped 48.9–68.4%. Clipping treatments to evaluate effects of use on yearly productivity were light use (13.3–24.7%) and total use (clipped to ground) in early and mid-summer, and control. There was no difference in fall graminoid biomass between controls and quadrats clipped lightly in early summer and mid-summer and there was no

difference in forb or graminoid yield (seasonally clipped herbage plus end of season herbage) in clipped quadrats and controls. Across years, forbs and graminoids clipped to ground in early summer and mid-summer regrew by fall to no more than 19.2, 4.2, 24.7, and 10.0%, respectively, of the amount in control quadrats.

Objectives

1) Evaluate production, species richness, and use of herbaceous standing crop in meadow communities by cattle and wild ungulates during early summer, mid-summer, and fall, 1999 and 2000.
2) Estimate end of growing season (fall 1999 and 2000) meadow production and annual yield from plants clipped to light use levels (13.3–24.7%), total use (clipped to ground, or 100%), and protected from all grazing during early and mid-summer.

Findings and Implications

1) Previous grazing history and introduction of exotic species has affected mountain meadow species composition.
2) Compensation did not occur following clipping treatments and growth and regrowth were most likely promoted by subirrigated soils underlying meadows.
3) Managers should consider delaying cattle grazing until late summer on mountain meadows used consistently by elk in early summer.

Chapter 3

Elk, Mule Deer, Cattle, and Domestic Sheep Diet Relationships on Arid Montane Summer Range

Abstract

We evaluated elk, mule deer (*Odocoileus hemionus*), cattle, and domestic sheep diet selection and overlap on northeastern Nevada summer range from 1998–2000. Diet compositions were determined through microhistological fecal analysis. Elk spring diets

were the most diverse; elk selected about 60% forbs in summer; mule deer selected a summer diet of about 30% and 67% woody browse and forbs, respectively; and cattle and sheep summer diets were dominated by graminoids. We found no difference between years in selection of forbs, graminoids, and browse but did detect a difference in selection between ungulates. Cattle and sheep selected the highest ratio of grass to browse, while mule deer diets were lowest in grass to browse ratios. Summer deer and spring elk diets contained lower ratios of forbs to browse than cattle, sheep, or elk in summer. Group means differed between all diet pairs, except elk in spring with sheep in summer, elk in summer with deer and sheep, and cattle with sheep in summer. Lupines (*Lupinus* spp.) formed a major portion of elk, deer, and sheep diets. Highest diet overlap was between cattle and sheep and lowest between deer and cattle. Summer elk and deer diets overlapped moderately. Elk and sheep apparently adjusted diets to cope with changing forage availabilities precipitated by drier weather in 2000. Shared Great Basin summer ranges should be managed to retain high natural diversity of forage plants. Increasing elk populations could elevate diet overlap and potentially lead to competitive interactions with mule deer, sheep, and possibly cattle.

Objectives

1) Investigate elk, mule deer, cattle, and domestic sheep diet relationships on shared northeastern Nevada summer range over 3 years.
2) Describe food niche overlap among this suite of ungulates.
3) Identify potentially competitive foraging scenarios for these herbivores on shared, arid montane summer ranges.

Findings and Implications

1) Elk and mule deer diets were largely composed of forbs and browse, while cattle and domestic sheep diets were primarily graminoids.

2) Moderate diet overlap occurred between elk and domestic sheep and elk and mule deer; however, current elk population and grazing levels do not appear to produce competitive foraging interactions. Increasing elk densities could elevate diet overlap with mule deer and sheep, and possibly cattle, and lead to competitive interactions.
3) Arrowleaf balsamroot (*Balsamorhiza sagittata*), bluebunch wheatgrass (*Pseudoroegneria spicata*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), mountain brome (*Bromus marginatus*), needlegrasses (*Achnatherum* spp.), snowbrush ceanothus (*Ceanothus velutinus*), and spurred lupine (*L. caudatus*) should be monitored due to their importance in elk diets.

Chapter 4

Nutrient Evaluation for Elk Forages on Northeastern Nevada Summer Range

Abstract

We compared crude protein, digestible energy (DE), calcium, magnesium, phosphorous, potassium, sodium, and sulfur levels in 12 common elk forage species in the Jarbidge Mountains of northeastern Nevada to optimal performance levels for lactating cow elk in early summer, mid-summer, and early fall 1999 and 2000. Species included 2 forbs: arrowleaf balsamroot and spurred lupine; 6 grasses: bluebunch wheatgrass, Idaho fescue (*Festuca idahoensis*), Kentucky bluegrass (*Poa pratensis*), mountain brome, needlegrasses, and Sandberg bluegrass (*P. secunda*); and 4 woody species: aspen (*Populus tremuloides*), curlleaf mountain mahogany, mountain snowberry (*Symphoricarpos oreophilus*), and snowbrush ceanothus. Spurred lupine and snowbrush ceanothus were the most proteinaceous plants, exceeding requirements across all seasons. By mid-summer, protein levels in all grasses were below elk requirements (12%). With the exception of curlleaf mountain mahogany in mid-summer, DE in woody browse met cow elk requirements in all seasons. Digestible energy in herbs demonstrated a marked decline from early summer through early fall, and no forb or grass satisfied elk requirements by early fall (2,750 kcal/kg). Sodium

levels never exceeded about 10% of the required 600 µg/g. The extent to which elk diet quality declines as overall forage quality declines was unclear, but it was clear that the potential for maintaining a relatively high density of elk at dietary quality levels that fulfill requirements declines as summers progress on northeastern Nevada summer ranges.

Objectives

1) Estimate seasonal crude protein, digestible energy, and macromineral levels in common elk summer forage species.
2) Evaluate whether forage plant nutrient levels met seasonal lactating cow elk requirements across summers.
3) Discuss nutritional findings and provide management implications in relation to elk population growth.

Findings and Implications

1) In general, macrominerals were widely available to elk.
2) Crude protein and digestible energy decreased in herbs and woody browse across summer seasons.
3) Digestible energy was the most limiting nutrient with woody browse only providing levels meeting lactating cow elk requirements in early fall.
4) Northeastern Nevada summer ranges must be managed to maintain a high diversity of plants for elk because nutrient levels wane in early fall.

Chapter 5

Habitat Use Constraints on Elk Summer Nutritional Carrying Capacity Estimates

Abstract

We estimated economic nutritional carrying capacity (I_{NCC}) for 236-kg cow elk in autumn 1999 and 2000 to reflect expected animal performance under reasonable extreme ranges in digestible energy. Maintenance performance (2,550 kcal/kg) was the DE level

required to maintain endogenous energy levels, particularly body fat levels, of adult cows with calves at heel. Optimal performance (2,750 kcal/kg) was the level where animals would be assured to experience no, or virtually no, limitations from nutrition. We used resource selection functions to redistribute I_{NCC} densities (RSFDs) for aspen, conifer, mahogany, sagebrush–herb, and snowbrush communities across the summer range and then adjusted original I_{NCC} estimates according to these RSFDs. We used a conditional fixed effects model to evaluate habitat selection between 136 elk cow group locations and 136 random, paired locations within 2.3 km buffers representing median distance moved between all aerial relocations. We approximated autumn 1999 to be 53 days and autumn 2000 to be 76 days. Maintenance performance I_{NCC} estimates for 236-kg lactating cow elk were 2,533 (95% CI: 1,277–3,789) in 1999 and 1,655 (95% CI: 856–2,454) in 2000. Optimal performance I_{NCC} estimates for 236-kg lactating cow elk were 2,264 (95% CI: 1,104–3,424) in 1999 and 1,100 (95% CI: 348–1,852) in 2000. Akaike's information criterion bias-correction for small samples identified the best binary logistic regression model explaining elk habitat selection. The best model, which included the natural log ratio of aspen to conifer cover types in each buffer and the nearest distance to a perennial stream from buffer centers, provided evidence in support of water and forage availability influencing habitat selection. Cross validation modeling indicated our model was a strong, positive predictor of elk habitat selection. Percentage cover type in 2.3-km elk buffers was comprised of higher aspen and snowbrush and less conifer than available as evaluated in random 2.3-km buffers. There was no difference between elk-used and random locations for cool aspect (N, E, NE, NW), elevation, mahogany cover, or sagebrush–herb cover. Decreases in I_{NCC} for 1999 and 2000 and at both performance levels were attributed to more cow elk predicted by RSFDs to be in aspen and sagebrush–herb communities than predicted by I_{NCC}. Each year, RSFDs predicted fewer elk would use conifer, mahogany, and snowbrush communities than original I_{NCC} models.

Objectives

1) Estimate economic nutritional carrying capacity for 236-kg lactating cow elk on summer range at 2 animal performance levels.
2) Model cow elk group summer habitat selection with resource selection functions.
3) Adjust carrying capacity estimates with resource selection functions to reflect probabilities of habitat selection.

Findings and Implications

1) Availability of aspen and free water largely influenced cow elk group habitat selection.
2) Dry autumn conditions in 2000 coupled with reduced forage and nutrient levels resulted in I_{NCC} estimates lower than in 1999. Maintenance performance I_{NCC} estimates were 34.7% lower and optimal performance I_{NCC} estimates were 51.4% lower in 2000 than in 1999.
3) Adjusted maintenance performance I_{NCC} estimates corresponded to 29.6% and 27.6% decreases in original 1999 and 2000 I_{NCC} estimates, respectively. Adjusted optimal performance estimates corresponded to 28.1% and 43.5% decreases in original 1999 and 2000 I_{NCC} estimates, respectively.
4) Elk populations maintained at original I_{NCC} estimates would have contributed to alteration of aspen and sagebrush–herb communities.
5) The 2000 maintenance performance I_{NCC} estimate adjusted with RSFDs (1,199) should serve as a benchmark for the Jarbidge population.

Appendix 1

Elk Habitat Availability Map: Development and Accuracy Assessment

Abstract

We used Landsat 7 ETM+ scenes to create a habitat availability map representing 5 major cover types including aspen, curlleaf mountain mahogany, sagebrush (*Artemisia* spp.), snowbrush ceanothus, and conifer consisting primarily of subalpine fir (*Abies lasiocarpa*), and limber (*Pinus flexilis*) and whitebark (*P. albicaulis*) pines in the Jarbidge Mountains of

northeastern Nevada. Composition for the summer range from reclassified Landsat 7 ETM+ data was 15.1% aspen, 10.7% conifer, 19.7% mahogany, 51.8% sagebrush, and 2.7% snowbrush. Overall, the composition of summer range consisted of more forested habitats and less sagebrush habitats as compared to the entire study area. We detected 89.6% map accuracy within 100-m buffers around 125 points classified from ground in 1998.

Appendix 2

Summer Nutritional Carrying Capacity Model for Elk in the Jarbidge Mountains, Nevada

Abstract

This appendix describes the development of our elk nutritional carrying capacity model. Our carrying capacity and variance estimators appear first and are then followed by 5 sections that define and detail major portions of our nutritional carrying capacity model. Methods and pertinent results are reported in each section, and, where needed, we provide introductory explanations. We also provide an analysis of the sagebrush–herb area most likely used by elk. This area could be used to further adjust carrying capacity estimates.

CHAPTER 1

ELK POPULATION CHARACTERISTICS, NEVADA DIVISION OF WILDLIFE HUNT UNIT 072, 1990–2003

INTRODUCTION

Bighorn (*Ovis canadensis*), bison (*Bison bison*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) are all native ungulates of northern Nevada (Zeveloff and Collett 1988, Krausman and Shackleton 2000, O'Gara and Dundas 2002). Archaeological excavations in Oregon and Nevada indicate elk were present post-Pleistocene in the Great Basin (Nevada Division of Wildlife 1997). Early researchers reported elk were probably infrequent in the state (Hall 1946) or Nevada was outside "normal" elk range (Murie 1951); their comments were attributed to a scarcity of historical accounts of elk in Nevada. Historical sightings of elk have been reported from the Bruneau, Jarbidge, and Independence Mountains in Elko County and the Schell Creek and Snake Mountains in White Pine County (Hall 1946, Murie 1951, Nevada Division of Wildlife 1997). Early newspapers reported kills at Lake Tahoe and Honey Lake Valley in western Nevada and in the Jarbidge and Independence Mountains in northeastern Nevada (Nevada Division of Wildlife 1997).

Elk were extirpated in Nevada by the end of the nineteenth century (Nevada Division of Wildlife 1997). Nevada sportsmen's organizations were responsible for the first release of 30 elk from Yellowstone National Park into the Schell Creek Range in 1932. The second translocation of elk occurred in 1935. This translocation consisted of 21 Yellowstone National Park elk released into the Charleston Mountains of Clark County (Bryant and Maser 1982). In spite of these early releases, many believed habitat was not suitable for elk to flourish in Nevada. A report to the Nevada Legislature considered elk habitat in northern Nevada to be submarginal due to joint use by livestock and big game even though elk were noted to formerly be present in fair numbers (Nevada Legislative Counsel Bureau 1959). The belief that habitat was not suitable to elk was further asserted by the Nevada Legislative Counsel Bureau (1959:98) when they stated, "Nevada is not elk country."

Recent expansion of elk in Nevada is largely a result of changes in societal attitudes precipitated by sportsmen's groups, primarily the Rocky Mountain Elk Foundation (Nevada Division of Wildlife 1997). Through 1996, 700 elk have been released at 8 sites in Nevada including the Bruneau River, Goshute Reservation, Jarbidge Mountains, Pilot Peak, Monitor Range, Schell Creek Range, South Egan Range, and Spring Range (Nevada Division of Wildlife 1997). Pioneering elk from these releases have also colonized new areas in the state (Lister and Baker 1996, Nevada Division of Wildlife 1997). Reintroduced elk increased to a statewide estimate of 3,335 by 1995 (Bunnell 1997) and reportedly further increased to a spring, precalving estimate of 5,300 by 1998 (G.A. Tanner, NDOW, personal communication, 1999, as cited in O'Gara and Dundas 2002).

In 1981, the Humboldt National Forest and Bureau of Land Management (BLM) Elko District Office prepared an environmental assessment entitled <u>Environmental Assessment for the Release of Elk into the Jarbidge Mountains</u>, prior to reintroduction of elk into the Jarbidge Mountains (U. S. Forest Service 1981). An ensuing cooperative agreement, known as the <u>Six Party Agreement for Elk Reintroduction in the Jarbidge Mountains, Nevada</u>

between the 71 Livestock Grazing Association and 5 natural resource agencies including NDOW, USDA Humboldt-Toiyabe National Forest, Idaho and Nevada BLM, and the Idaho Department of Fish and Game led to the reintroduction of 93 elk into the Jarbidge Mountains of northeastern Nevada from 1990 to 1995 (Table 1). This agreement expired in December 1999. Reintroduction efforts were intended to establish a target population of 300 elk wintering at 2 locations. Hunting strategies were implemented in 1994 to maintain this population near 300; this level was reached in 1996 (Fig. 1). New population objectives call for the population to increase to 1,000 ± 100 by 2010 (Nevada Division of Wildlife 2000*a*).

Three releases of 93 elk were distributed between north and east release sites from 1990 to 1995. The north site was at Cougar Point near Robinson Hole on the East Fork of the Jarbidge River and the east site was in the O'Neil Basin. The first three releases were at Cougar Point. Forty-seven elk (20 captured near Montrose, Colorado; 27 captured in the Oquirrh Mountains of Utah) were released at this site in January and February 1990 (Table 1). A series of three releases occurred at the east site in January 1991. These releases were of 31 elk captured in the Oquirrh Mountains. A final release was made into the O'Neil Basin in February 1995 of 15 elk captured in the Elkhorn Wildlife Area, northeastern Oregon (Table 1). Radio telemetry work demonstrates Hunt Unit 072 provides year-round elk habitat and elk do move in and out of the unit indicating these elk do not exist as a closed population (unpublished data, J. Williams, personal communication, 1998). Our objective was to provide an analysis and synthesis of population information for elk reintroduced into the Jarbidge Mountains of northeastern Nevada in the 1990s.

STUDY AREA

The study area comprises Nevada Division of Wildlife (NDOW) Hunt Unit 072 (41º 30' to 42º 00' N and 115º 00' to 115º 30' W) in northeastern Nevada. Hunt Unit 072 consists of 1,665 km^2 with elevations ranging from 1,633 to 3,287 m. We delineated all area ≥2,135 m as elk summer range because 91.3% of cow elk groups relocated on radiotelemetry flights across summers 1998–2001 were found in this region. Summer range includes 48.2%, or 802 km^2 of the study area, and is administered by Forest Service (91.5%), Bureau of Land Management (5.4%), and private ownership (3.1%). The 392 km^2 U.S. Forest Service Jarbidge Wilderness Area comprises most of the Jarbidge Mountains and 48.9% of the summer range. Northern slopes drain into the Snake River, while southern slopes drain into the Great Basin (U.S. Forest Service 1981). Principal land use was summer and early fall grazing on 1 common use, 11 domestic sheep, and 33 cattle allotments.

Late fall through mid-spring snowpack provides most moisture. Snow water equivalents on 1 April at Natural Resources Conservation Service SNOTEL sites at Draw Creek (2,300 m) in the south, and Pole Creek Ranger Station (2,540 m) in the north were 88 and 104%, and 91 and 90% of 1971–2000 averages (Draw Creek, 297 mm; Pole Creek, 523 mm) in 1999 and 2000, respectively. Mean monthly temperatures (ºC) averaged from June through October were 11.3 ± 2.1 in 1999 and 13.6 ± 2.0 in 2000 at Draw Creek and 9.6 ± 2.4 in 1999 and 11.4 ± 2.0 in 2000 at Pole Creek Ranger Station. June through October cumulative precipitation (mm) was 104 and 102, and 41 and 51, in 1999 and 2000 at Draw Creek and Pole Creek Ranger Station, respectively.

Mountain big sagebrush (*Artemisia tridentata vaseyana*) and low sagebrush (*A. arbuscula*) interspersed with herbaceous meadows and snowbank associations form a matrix between forested communities. Forested communities include aspen (*Populus tremuloides*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), snowbrush (*Ceanothus velutinus*), and a conifer complex consisting primarily of subalpine fir (*Abies lasiocarpa*), limber pine (*Pinus flexilis*), and whitebark pine (*P. albicaulis*). Lewis (1975) provided lists of herbaceous species in each community.

Elk share summer range in the Jarbidge Mountains with mule deer and pronghorn. Mule deer densities averaged 7.9/km^2 from 1998 to 2000 across Hunt Unit 072 (L. Gilbertson, Nevada Department of Wildlife, personal communication 2003). Potential predators of elk include bobcat (*Felis rufus*), coyote (*Canis latrans*), and mountain lion (*Felis concolor*). Gray wolves (*C. lupus*) are native to Nevada, but were extirpated by early settlers (Zeveloff and Collett 1988, Ballard and Gipson 2000). Black bear (*Ursus americanus*) and wolverine (*Gulo gulo*) are also native to the Jarbidge area and were likewise extirpated by the early 1900s (Zeveloff and Collett 1988, Gruell 1998).

METHODS

Summer Elk Population Composition

Cow elk were captured on winter ranges in 1998 and 2000 with netguns shot from helicopters to facilitate attachment of VHF radio collars (Telemetry-Electronics Consultants, Inc., Mesa, Arizona, USA). Ten cow elk were captured on winter ranges in the East Fork of the Jarbidge River drainage in the northern portion of the study area on 28 March 1998. Five of these cows were harvested during 1998 and 1999. On 29 March 2000, an additional 3 cow elk were captured and radio-collared on the East Fork of the Jarbidge River drainage and 4 cow elk were captured and radio-collared on the east slope of the Jarbidge Mountains. The increased capture area in 2000 was necessitated by a mild winter that resulted in a larger area of elk distribution. Radio-collared cows provided locations of elk groups composed primarily of cows, calves, and yearling bulls.

Flights to relocate collared cow elk were conducted during summers 1998–2000 by an NDOW wildlife biologist. Locations with accompanying Universal Transverse Mercator coordinates and general community types were recorded where elk groups were located. Our field crews used this information to locate elk on the ground. Groups represented by radio-collared animals and some general observations of elk groups were included in population classification summaries to increase samples. We used spotting scopes and binoculars to classify all elk groups observed from May through mid-September according to cows, calves, yearling bulls, branch-antlered bulls, or unclassified as to sex and age. Population ratios were only calculated from those groups where all elk were visible from 1 July to mid-September. Classifications after 1 July are most appropriate to include in population ratios, as calves are most observable following 1 July even though numbers may be higher in June (Raedeke et al. 2002). One group classified in 1998 and 3 groups classified in 1999 with a cow collared on Jarbidge winter range were found in the Buck Creek area, in adjacent Hunt Unit 071. We included these 3 groups in summer sex and age ratio calculations. We did not classify elk after the opening of mid-September rifle elk hunting seasons due to behavioral and herd compositional changes following hunting pressure.

Nevada Division of Wildlife Elk Population Monitoring

Nevada Division of Wildlife conducted helicopter flights to survey annual winter elk herd composition. Composition flights typically were conducted 2 to 3 days after a fresh

January or February snowfall. Pilots followed tracks in snow to locate elk concentrations on winter range. Attempts were made to locate elk on major wintering areas to increase the sample of animals counted and to adequately represent population structure. A NDOW biologist recorded numbers of cows, calves, and bulls observed in elk concentrations. Counts were then used to compute ratios of calves to 100 cows, bulls to 100 cows, and calves to 100 adults (J. Williams, NDOW, personal communication 2003).

Big game hunters in Nevada are required to report harvest statistics to NDOW following hunts. Mandatory hunter reports require hunters to report whether they killed an animal, sex of harvested animal, date of kill, and antler points if a male was harvested. J. Williams, NDOW wildlife biologist, computed annual one-point-in-time pre-hunting population estimates for Hunt Unit 072. Estimates were computed for 15 ages with POP-II (Fossil Creek Software, Fort Collins, Colorado) a population-modeling program. Models depicted population size in August, prior to hunting seasons. Parameters entered into models included number of animals in the previous year's estimate, mortality rates, animals harvested in the hunting unit the previous fall, and population production, represented through cow to calf ratios. Mortality rates included predation and crippling losses incurred as a result of hunting. Crippling loss was typically considered to be 40% of the harvest for all classes harvested during previous fall hunts. Cow to calf ratios were adjusted downward from winter helicopter composition flights following harsh winters (J. Williams, NDOW, personal communication 2003).

We computed lambda (λ [N_{t+1}/N_t]), the finite rate of increase, for each year to evaluate population growth rates; geometric mean growth rates were then calculated to evaluate growth when antlerless hunting was undertaken (1995–1999) and following closure of antlerless seasons (2000–2003). We also computed population doubling (ln[2]/ln[λ]) and tripling (ln[3]/ln[λ]) times using the geometric mean λ from 2000–2003 to provide predictions of population growth (Akçakaya et al. 1999).

RESULTS AND DISCUSSION

Summer Elk Population Composition

Total individual elk classified at ground observations from late May to mid-September were 1,466 in 1998; 784 in 1999; and 685 in 2000. Herd composition ratios were calculated from 721 elk in 28 groups (mean group size = 25.8 ± 7.8; mean ± SE; range = 1–214) in 1998; 518 elk in 35 groups (mean group size = 14.8 ± 2.9; range = 1–81) in 1999; and 192 elk in 27 groups (mean group size = 7.1 ± 1.9; range = 1–44) in 2000 (Table 2). Largest groups observed each year were in the Mary's River Basin in the southeastern portion of the Jarbidge Wilderness Area: 214 in 1998; 81 in 1999; and 147 in 2000. All animals in largest groups in 1999 and 2000 were not classifiable as to sex and age and were not included in calculations. A large nursery herd formed in this area during early summer and remained until the rut in September. Another large nursery group of 81 elk was found in the Buck Creek allotment in Hunt Unit 071 in 1999 and were included in composition ratios. It is unclear why average herd size decreased by about 50% each year from the preceding year. It is possible that drier weather conditions induced animals to form smaller groups in search of limited forage.

Calves per 100 cows ratios from 1 July to mid-September averaged 52 (range = 32–57) from 1998 to 2000 (Table 2). Mean ratios as high as 79 calves per 100 cows were reported for a newly established population in southcentral Washington shrub-steppe habitat

(Eberhardt et al. 1996). However, elk populations with ratios of more than 50 calves per 100 cows recruited into the population suggest productive, growing populations with a younger adult female age structure (Wisdom and Cook 2000). Calves per 100 cows in 2000, an index of productivity, decreased 43.9 and 39.6% from ratios in 1998 and 1999, respectively. Lowest calf production (32 per 100 cows) was found in summer 2000. Lower calf numbers in 2000 may have reflected dry, windy conditions in early summer that adversely affected foraging conditions leading to lower calf survival (Chapter 4; Appendix 2). Bulls per 100 cows on summer range varied between 27 in 1998 to 46 in 2000 (Table 2). On average, there were 17 branch-antlered bulls (range = 12–25) and 17 yearling bulls (range = 15–21) per 100 cows across summers 1998–2000 (Table 2).

Winter Elk Population Composition

Winter herd composition best reflects recruitment of calves into the population because winter composition ratios account for the effects of fall hunting and a portion of winter mortality. In addition, loss of calves during severe winters is accounted for in the NDOW population estimate model. Two primary goals of elk managers are to increase the ratio of mature males to females and the ratio of calves to females. Populations with high numbers of males and calves relative to adult females are productive and optimize hunting opportunities (McCullough 1994, Wisdom and Cook 2000). Hunting is a factor in lower bull to cow ratios in winter as compared to summer as at least 90% of antlered elk mortality occurs during hunting seasons (Skovlin et al. 2002). Furthermore, most bulls in hunted populations live less than 5 years and in some cases less than 2 (Wisdom and Cook 2000).

Five-year winter averages of calves per 100 cows increased from 45 in 1992–1996 to 48 in 1997–2001, while 5-yr average bulls per 100 cows increased from 29 to 30 over the same periods (Table 3). These ratios are slightly higher than a statewide average of 25 bulls per 100 cows and 42 calves per 100 cows (Nevada Division of Wildlife 1997). Composition ratios are not tied to population size, so it is not wise to infer changes in population productivity from ratio data. For example, an increase in young to female ratios may be a factor of heavy adult mortality coupled with density-dependent increase in calf recruitment. A biologist may mistake this phenomenon as an increase in the population, when in fact it is really just a change in population structure (McCullough 1994).

Population ratios in summer and winter generally agreed and indicate that the elk herd in Hunt Unit 072 is productive. Herd composition counts are based on the fact that adult females are the basis of comparison. Assumptions for this approach to work are "(1) that female recruitment and mortality are relatively stable as compared to male recruitment and mortality, and (2) that female mortality is small relative to offspring mortality" (McCullough 1994:299). Elevated anterless elk harvests from 1996 to 1998 may have skewed ratios toward higher numbers of calves and are reflected in higher winter calf to 100 cow ratios following these hunts (Tables 3 and 4). The lagged response of male to 100 adult female ratios in increasing juveniles per 100 adult females has been substantiated for elk and mule deer in a Colorado study (White et al. 2001). Observed ratios indicated 0.28 and 0.18 calves per 100 cows in response to each 1 bull per 100 cows preharvest increase the previous fall and 2 previous fall's, respectively (White et al. 2001).

Elk Hunting

Elk hunting was initiated in 1994 when 3 bull permits were issued; 2 bulls were harvested during the first hunt. Harvest success for bull elk from 1994 to 2002 was 95 for 124 permits, or 76.6% (Table 4). Anterless elk harvesting began in 1995 when 8 hunters harvested 5 elk. Hunters harvested 118 of 463, or 25.5% of antlerless elk permits issued by NDOW from 1995 to 1999 (Table 4). Lower antlerless hunt success was largely attributed to elk moving into inaccessible portions of the roadless Jarbidge Wilderness in response to hunter pressure near roads (J. Williams, NDOW, personal communication).

Mortality rate is a simple division or ratio of number of deaths divided by the number in the sample during a specified period. Basic survival estimates are calculated as 1–(number of deaths/number at risk of death), or equivalently 1- mortality rate (Winterstein et al. 2001). However, the above type of survival estimate, referred to as apparent percent success (APS), does not consider censored animals or those animals that leave the study or are not found, thus their fate is unknown. More complicated procedures allow for staggered entry (i.e., not all individuals enter the study at the same time). Nine of 10 cows radio-marked in 1998 stayed year round in Hunt Unit 072. Of these, hunters harvested 2 in fall 1998, resulting in a mortality rate of 0.22 and an APS of 0.78. In 1999, hunters harvested 2 during fall hunts, resulting in a mortality rate of 0.29 and a corresponding APS of 0.71. All 4 elk deaths were inflicted by hunters, further supporting the importance of human hunters in controlling elk populations in northeastern Nevada. Seven additional cows were radio marked in 2000; however, the lone antlerless elk harvested in 2000 (Table 4) was not collared. Predation is unlikely to be a significant population depressant in northeastern

Nevada because: (1) there are no black bears or gray wolves, and (2) predation from extant predators such as cougars and coyotes has not appreciably altered rate of increase (Fig. 1).

An analysis conducted by the Bureau of Land Management (1995) provides an indication of the economic value of elk hunting for the local area. In 1993, 30 elk tags were allocated for the Wells Resource Area (BLM lands in Jarbidge Mountains included). These tags generated $21,500 in expenditures in Elko County and provided a 0.4 full-time equivalent job (800 hr of labor). An estimate indicated that the capitalized value of Nevada's elk resource exceeded $11,000,000 in 1995 (Nevada Division of Wildlife 1997:13–14). In addition, the 305 hunters pursuing elk in Nevada in 1995 spent an estimated minimum $341,600 (Nevada Division of Wildlife 1997). Elk viewing, antler collecting, and photography add additional recreational, aesthetic, and economic benefits to Nevada communities (Barber 1996, Nevada Division of Wildlife 1997).

Population Estimates and Growth Rates

Elk reached an initial population objective of 300 by 1996 and were maintained near this level through antlerless harvest until 1999 (Table 5; Fig. 1). Geometric mean finite rate of increase was $\lambda = 1.08$ (range = 0.98–1.23) during the period of antlerless elk hunting from 1995 to 1999 and increased to $\lambda = 1.15$ (range = 0.84–1.38) following release from antlerless hunting from 2000 to 2003 (Fig 1). In the absence of substantial cow harvests, this population is predicted to double to 1,110 animals in 5 years (2008) and to triple to 1,650 in about 8 years (2011) with current growth rates. Instantaneous rate of growth (r), calculated as $r = \ln(\lambda)$, provides a measure of annual percentage (reported as proportions) increase in the population. Mean instantaneous rate of growth from 1995 to 1999 was 0.08 per year and from 2000 to 2003 was 0.14 per year. By comparison, a 20-yr reproductive and survival trend data set from elk that colonized the U.S. Department of Energy, Hanford Site, south-central Washington, demonstrated long-term growth rates of $r = 0.20$ ($\lambda = 1.22$; Eberhardt et al. 1996). Eberhardt et al. (1996) suggested a feasible maximum sustainable growth rate for elk may be as high as $r = 0.28$ ($\lambda = 1.33$). Elk in Yellowstone National Park, Wyoming, have reached a stable age distribution, are constrained by density dependence, and grew at a rate of $\lambda = 1.09$ from 1968 to 1988 (Singer et al. 1998).

Productivity and survival largely influence population growth (Akçakaya et al. 1999); thus estimates of these vital rates are extremely useful when evaluating management and population objectives. For example, elk population response simulations conducted by Nelson and Peek (1982) revealed the order of magnitude effect on λ from greatest to lowest was adult survival, calf and yearling survival, adult fecundity, and yearling fecundity. Wildlife biologists thus must understand the relative contribution of various forms of mortality on animals throughout different life stages to make meaningful interpretations of survival estimates. Furthermore, it is highly likely that inadequate information on survival and fecundity parameters influenced NDOW population estimates and, subsequently, growth rates. High variation in growth rates following closure of antlerless elk seasons in an area with few natural predators and mild winter conditions is inconsistent with a growing elk population. Lambdas as low as 0.84 in 2000 arguably mask the true growth of this population, and the lack of confidence intervals around population estimates provide further evidence that the elk population in Hunt Unit 072 is much larger than it is estimated to be.

LITERATURE CITED

Akçakaya, H. R., M. A. Burgman, and L. R. Ginzburg. 1999. Applied population ecology: principles and computer exercises using RAMAS® EcoLab 2.0. Second edition. Applied Biomathematics, Setauket, New York, USA.

Ballard, W. B., and P. S. Gipson. 2000. Wolf. Pages 321–346 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Barber, M. J. 1996. Ely elk viewing interpretive area: elk and cattle at home on the range. Pages 110–111 *in* K. E. Evans, compiler. Sharing common ground on western rangelands: proceedings of a livestock/big game symposium. U.S. Forest Service General Technical Report INT-GTR-343.

Bryant, L. D., and C. Maser. 1982. Classification and distribution. Pages 1–59 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Bunnell, S. D. 1997. Status of elk in North America: 1975–1995. Rocky Mountain Elk Foundation, Missoula, Montana, USA.

Bureau of Land Management. 1995. Wells resource management plan: proposed elk amendment and environmental assessment. U. S. Department of the Interior, Bureau of Land Management, Elko District, Wells Resource Area Office, Elko, Nevada.

Eberhardt, L. E., L. L. Eberhardt, B. L. Tiller, and L. L. Caldwell. 1996. Growth of an isolated elk population. Journal of Wildlife Management 60:369–373.

Gruell, G. E. 1998. Northern Elko County: the way it was. Northeastern Nevada Historical Society Quarterly 98-4:105–126.

Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, California, USA.

Krausman, P. R., and D. M. Shackleton. 2000. Bighorn sheep. Pages 517–544 *in* S. Demarais and P. R. Krausman, editors, Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Lewis, M. E. 1975. Plant communities of the Jarbidge Mountain complex, Humboldt National Forest. Report to Intermountain Region, U.S. Forest Service, Ogden, Utah, USA.

Lister, R., and B. Baker. 1996. Wells resource management plan elk amendment. Pages 73–76 *in* K. E. Evans, compiler. Sharing common ground on western rangelands:

proceedings of a livestock/big game symposium. U.S. Forest Service General Technical Report INT-GTR-343.

McCullough, D. R. 1994. What do herd composition counts tell us? Wildlife Society Bulletin 22:295–300.

Murie, O. J. 1951. The elk of North America. Teton Bookshop, Jackson, Wyoming, USA.

Nelson, L. J., and J. M. Peek. 1982. Effect of survival and fecundity on rate of increase of elk. Journal of Wildlife Management 46:535–540.

Nevada Division of Wildlife. 1997. Nevada elk species management plan. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 1998. Big game status and quota recommendations 1998. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 1999. Big game status and quota recommendations 1999. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2000*a*. Sub-plan for elk management in the Jarbidge Mountains, Nevada. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2000*b*. 1999 – 2000 big game status book. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2001. 2000 – 2001 big game status. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2002. 2001 – 2002 big game status. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2003. 2002 – 2003 big game status. Nevada Division of Wildlife, Reno, Nevada, USA.

Nevada Legislative Counsel Bureau. 1959. Survey of fish and game problems in Nevada. Bulletin Number 36. State Printing Office, Carson City, Nevada, USA.

O’Gara, B. W., and R. G. Dundas. 2002. Distribution: past and present. Pages 67–119 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

Raedeke, K. J., J. J. Millspaugh, and P. E. Clark. 2002. Distribution: past and present. Pages 67–119 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968–1993. Wildlife Society Bulletin 26:375–390.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–555 *in* D. E. Toweill, and J. W. Thomas, editors, North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

U.S. Forest Service. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. U.S. Forest Service, Humboldt National Forest, Elko, Nevada.

White, G. C., D. J. Freddy, R. B. Gill, and J. H. Ellenberger. 2001. Effect of adult sex ratio on mule deer and elk productivity in Colorado. Journal of Wildlife Management 65:543–551.

Winterstein, S. R., K. H. Pollock, and C. M. Bunck. 2001. Analysis of survival data from radiotelemetry studies. Pages 351–380 *in* J.J. Millspaugh, and J.M. Marzluff, editors, Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Wisdom, M. J., and J. G. Cook. 2000. North American elk. Pages 694–735 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zeveloff, S. I., and F. R. Collett. 1988. Mammals of the Intermountain West. University of Utah Press, Salt Lake City, USA.

Table 1. Record of Nevada Division of Wildlife elk translocations[a] into the Jarbidge Mountains, Nevada, 1990–1995.

Date	Release site	Capture location	Adult females	Yearling males	Calf females	Calf males	Total
01/22/1990	Cougar Point	Montrose, Colorado	15	4	0	1	20
01/27/1990	Cougar Point	Erda, Utah	7	1	0	2	10
02/15/1990	Cougar Point	Erda, Utah	10	1	1	5	17
01/1991[b]	O'Neil Basin	Erda, Utah	18	0	7	6	31
02/25/1995	O'Neil Basin	North Powder, Oregon	10	1	2	2	15
Total			60	7	10	16	93

[a] Data from Nevada Division of Wildlife (1997) and J. Williams, Nevada Division of Wildlife, personal communication, 1998.

[b] Three releases of 31 elk from Erda, Utah occurred in January 1991. The first release was of 10 elk, the second 16, and 5 elk were translocated on the third release.

Table 2. Summer elk population composition, Nevada Division of Wildlife, Hunt Unit 072, 1 Jul to mid-Sep, 1998–2000. Elk classified from ground counts of *n* = 28 groups in 1998, *n* = 35 groups in 1999, and *n* = 27 groups in 2000. All animals in each group were classifiable to sex and/or age group.

Year	Counts						Ratios (per 100)				
	Yearling bulls	Branched bulls	Total bulls	Cows	Calves	Total elk	Calves : cows	Calves : adults	Bulls : cows	Yearling bulls : cows	Branched bulls : cows
1998	57	48	105	392	224	721	57	45	27	15	12
1999	51	58	109	267	142	518	53	38	41	19	22
2000	23	27	50	108	34	192	32	22	46	21	25
Mean	44	44	88	256	133	477	52	39	34	17	17
SE	10	9	19	82	55	154					

[b] Ratios for 3-yr means were calculated as: (average counts / average counts)*100. For example, 3-yr mean ratio for bulls : cows was: (3-yr mean bull count / 3-yr mean cow count)*100.

Table 3. Elk winter helicopter survey composition[a], Nevada Division of Wildlife, Hunt Unit 072, 1992–2003. Five-year averages are included for comparisons.

Year	Counts				Ratios (per 100)		
	Bulls	Cows	Calves	Total	Bulls : cow	Calves : cow	Calves : adult
1992	19	67	30	116	28	45	35
1993	26	48	22	96	54	46	30
1994	33	55	26	114	60	47	30
1995	25	113	31	169	22	27	22
1996	21	141	80	242	15	57	49
Mean	25	85	38	147	29[b]	45	34
SE	2	18	11	27			
1997	41	170	90	301	24	53	43
1998	25	134	68	227	19	51	43
1999	27	108	55	190	25	51	41
2000	46	95	47	188	48	49	33
2001	74	213	85	372	35	40	30
Mean	43	144	69	256	30	48	37
SE	9	21	8	36			
2002	45	215	102	362	21	47	39
2003	78	348	147	573	22	42	35

[a] Data for 1992–1997 provided by J. Williams, NDOW, personal communication 2002. Data for 1998–2003 from Nevada Division of Wildlife (1998, 1999, 2000*b*, 2001, 2002, 2003).

[b] Ratios for 5-yr means were calcuated as: (average counts / average counts)*100. For example, 5-yr mean ratio for bulls : cow was: (5-yr mean bull count / 5-yr mean cow count)*100.

Table 4. Elk hunting permit quotas and harvest[a], Nevada Division of Wildlife Hunt Unit 072, Jarbidge Mountains, Nevada, 1994-2002.

Year	Permit Quotas	Cumulative permit quotas	Number harvested	Cumulative harvested	Harvest Success %
Bull					
1994	3	--	2	--	66.7
1995	9	12	9	11	100.0
1996	9	21	8	19	88.9
1997	11	32	10	29	90.9
1998	14	46	11	40	78.6
1999	15	61	15	55	100.0
2000	21	82	18	73	85.7
2001	19	101	10	83	52.6
2002	23	124	12	95	52.2
Total					76.6
Antlerless					
1995	8	--	5	--	62.5
1996	50	58	16	21	32.0
1997	200	258	48	69	24.0
1998	200	458	48	117	24.0
1999	5	463	1	118	20.0
2000	0	463	0	118	--
2001	0	463	0	118	--
2002	0	463	0	118	--
Total					25.5

[a] Data for 1994–1997 provided by J. Williams, NDOW, personal communication 2003. Data for 1998–2003 from Nevada Division of Wildlife (1998, 1999, 2000*b*, 2001, 2002, 2003).

Table 5. Elk herd minimum population estimates (*N*)[a], Nevada Division of Wildlife, Hunt Unit 072, 1994–2003. Minimum estimates were computed with POP-II (Fossil Creek Software, Fort Collins, Colorado, USA).

Year	Adult males		Adult females		Juveniles		Total
	N	%	*N*	%	*N*	%	*N*
1994	30	0.171	100	0.571	45	0.257	175
1995	55	0.228	138	0.573	48	0.199	241
1996	58	0.195	147	0.495	92	0.310	297
1997	79	0.237	159	0.477	95	0.285	333
1998	99	0.305	142	0.437	84	0.258	325
1999	64	0.199	169	0.525	89	0.276	322
2000	52	0.192	146	0.539	73	0.269	271
2001	77	0.206	219	0.587	77	0.279	373
2002	84	0.191	252	0.573	104	0.236	440
2003	108	0.195	323	0.582	124	0.223	555

[a] Data for 1994–1997 provided by J. Williams, NDOW, personal communication 2003. Data for 1998–2003 from Nevada Division of Wildlife (1998, 1999, 2000*b*, 2001, 2002, 2003).

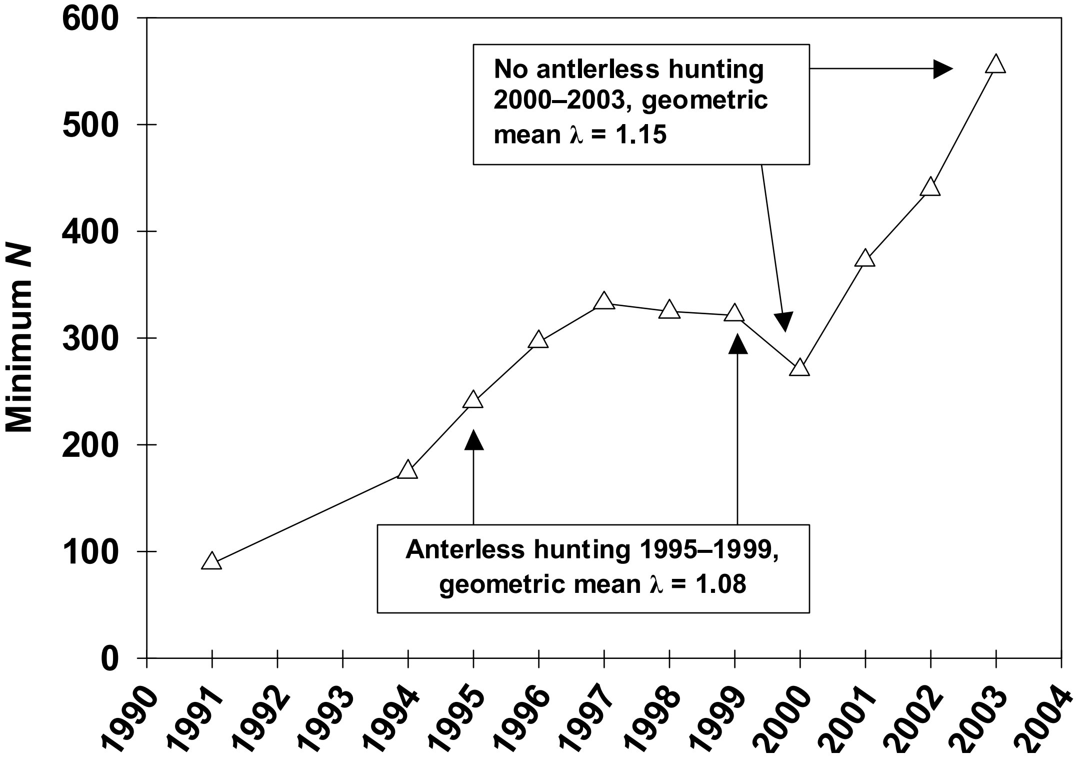


Fig. 1. Total elk population minimum estimates (N) and finite rate of increase (λ) during antlerless elk hunting (1995–1999) and following end of substantial cow harvests (2000–2003), Jarbidge Mountains, Nevada, 1991–2003. Objectives from the Six Party Agreement for Elk Reintroduction in the Jarbidge Mountains, Nevada, called for the population to be maintained at 300 adults until 1999.

CHAPTER 2

HERBAGE PRODUCTIVITY AND UNGULATE USE OF NORTHEASTERN NEVADA MOUNTAIN MEADOWS

INTRODUCTION

Mountain meadows occur on about 1,618,800 ha (~50% private and ~50% public lands) across the western United States (Gomm 1979). Where available, they provide an extremely productive, nutritious, and reliable forage resource (Reid and Pickford 1946, Patton and Judd 1970). For example, moist mountain meadows on forested summer range in eastern Oregon and eastern Washington comprise only 1–2% of the area, however, they may produce upwards of 20% of summer range forage (Reid and Pickford 1946). Wet mountain meadows are typically flooded in spring and are therefore dominated by flood-tolerant graminoids and to a lesser extent by a variety of forbs (mostly non-legumes), and a few phreatophytic shrubs (Cooper et al. 1957, Gomm 1979). As summer progresses, cattle are drawn to mountain meadows where forage quality is sustained longer than in surrounding communities (Reid and Pickford 1946). Higher quality forage persists because mountain meadows are either subirrigated by springs (wet meadows) or fed by melting snow (dry meadows). Consequently, calves, yearlings, and adult cattle grazing meadows have demonstrated higher weight gains than cattle grazing adjacent upland areas (Cooper et al. 1957, Clanton and Burzlaff 1966).

Elk (*Cervus elaphus*) rely heavily on mountain meadows in many areas for spring and early summer forage (Kowalsky 1964, Hayden-Wing 1979, Mantz 1993, Kelly 1995). Elk have recently been reestablished and (or) are colonizing the mountain ranges of northeastern Nevada (Nevada Division of Wildlife 1997). Concern has been expressed over impacts of these new elk populations grazing mountain meadows because meadows are a major source of cattle forage in Nevada (Hackett 1984).

Herbaceous mountain meadows interspersed among mountain big sagebrush (*Artemisia tridentata vaseyana*) and low sagebrush (*A. arbuscula*) communities in northeastern Nevada provide forage throughout summer to livestock and wildlife including elk, mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), white-tailed jackrabbit (*Lepus americanus*), ground squirrels (*Spermophilus* spp.), and greater sage-grouse (*Centrocercus urophasianus*). Livestock grazing has been the dominant summer use of northeastern Nevada mountain rangelands since cattle ranching began following the Civil War (Timothy 1980, Young and Evans 1989, Gruell 1998). Mountain meadows in the region were commonly hayed to provide winter cattle forage (Young and Evans 1989, Gruell 1998). Cattle, domestic sheep, and horses owned by local producers competed for summer forage with large, out-of-state sheep bands in the late 1800s and early 1900s (Timothy 1980, Young and Evans 1989, Gruell 1998). Grazing practices have largely healed early grazing abuses since designation of mountain rangelands as National Forest Reserves in the early 1900s (Timothy 1980, Gruell 1998).

We examined annual productivity and use of mountain meadows by wildlife (mainly big game) and cattle in and adjacent to meadow exclosures in northeastern Nevada. Our primary objectives were to evaluate: (1) production, species richness, and use of herbaceous standing crop in meadow communities by cattle and wild ungulates during early summer, mid-summer, and fall, 1999 and 2000, and (2) end of growing season (fall 1999 and 2000) meadow production and annual yield from plants clipped to light use levels (13.3–24.7%), total use (clipped to ground, or 100%), and protected from all grazing during early summer and mid-summer.

STUDY AREA

Our 166,500 ha study area was located in northeastern Elko County, Nevada (Fig. 1). The Humboldt-Toiyabe National Forest (HTNF), Jarbidge Ranger District comprised 94,226 ha (56.6%), Bureau of Land Management 35.9%, and private lands 7.5 % of the study area. Elevation ranged from 1,633 to 3,287 m. Soils across the study area were formed from igneous parent material (rhyolite and basalt; U.S. Forest Service 1981, Manning and Padgett 1995). The northern slope of the Jarbidge Mountains drains into the Snake River, while south slopes drain into the Great Basin. Deposition of rhyolitic boulders in high elevation glacial cirques has rendered subalpine sites porous and droughty (Loope 1969, Manning and Padgett 1995), consequently, most meadows occur at lower elevations.

Snowpack accumulated from late fall through mid-spring provides most moisture. Snow water equivalents on 1 April at Natural Resources Conservation Service SNOTEL sites at Draw Creek (2,300 m) in the south, and Pole Creek Ranger Station (2,540 m) in the north and near the meadow communities, was 88 and 104%, and 91 and 90%, of 30-yr (1971–2000) averages (Draw Creek, 297 mm; Pole Creek, 523 mm) in 1999 and 2000, respectively. Mean monthly temperatures (ºC) averaged from June through October were 11.3 ± 2.1 in 1999 and 13.6 ± 2.0 in 2000 at Draw Creek, and 9.6 ± 2.4 in 1999 and 11.4 ± 2.0 in 2000 at Pole Creek Ranger Station. June through October cumulative precipitation was 104 and 102 mm, and 41 and 51 mm, in 1999 and 2000 at Draw Creek and Pole Creek, respectively.

Rocky Mountain elk (*C. e. nelsoni*) were reintroduced into the Jarbidge Mountains from 1990–95 (Nevada Division of Wildlife 1997) and a population of about 300 (density = 0.18/km^2) was maintained by antlerless harvest from 1996–2000 (Chapter 1). Elk shared summer range with mule deer, pronghorn, cattle, and domestic sheep. Principal land use was summer and early fall grazing on 1 common use, 11 domestic sheep, and 33 cattle allotments.

Mountain big sagebrush and low sagebrush interspersed with herbaceous meadows and snowbank associations form a matrix between forested summer range communities. Forested communities include aspen (*Populus tremuloides*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), snowbrush (*Ceanothus velutinus*), and a conifer complex consisting primarily of subalpine fir (*Abies lasiocarpa*), limber pine (*Pinus flexilis*), and whitebark pine (*P. albicaulis*). Vegetation coverage from Nevada GAP, a geographical database (Scott et al. 1993), indicates mountain meadow communities comprised ≤0.2% of the area.

We evaluated 3 meadow communities, Black Spring, Monument Spring, and a meadow community north of Sagehen Spring, hereafter Sagehen Spring, that were partially fenced with 1.07-m high, 4-strand barbwire fences to exclude spring water sources from cattle (Fig. 1). Springs were piped to provide water in troughs outside spring exclosures. The fence around Monument Spring was erected in 1994, and fences apparently were built around Black and Sagehen Springs in the 1980s (J. Speck, HTNF, personal communication 2003). Livestock and wildlife grazed these areas before fence placement, and wild herbivores currently graze areas inside the exclosures as well as in the adjacent unfenced areas. Forest Service personnel evaluated these meadow complexes during the course of our study to assess vegetation and soil water conditions. A scorecard based on vegetation frequency and rooting depth was used to assess similarity of each meadow community to its potential natural community (Weixelman et al. 1996).

Black Spring

Black Spring (41º 52.8' N, 115º 7.6' W; 2,246 m elevation; E aspect; 4.4% slope) is located in the HTNF Black Spring cattle allotment. Black Spring and Caudle Creek allotments (5,271 ha) were managed under a deferred rotation grazing system and stocked with cow/calf pairs at a rate of 0.82 animal unit months (AUM)/ha from 6 July through 11 October 1999, and 0.72 AUM/ha from 1 July through 16 September 2000. The cattle exclosure encompassed 0.3 ha around Black Spring. The meadow community at Black Spring was classified as a mesic graminoid/Aquic Cryoboroll/trough drainageway ecological type (Weixelman et al. 1996).

Common graminoids included Baltic rush (*Juncus balticus*), Columbia needlegrass (*Achnatherum nelsonii*), Douglas' sedge (*Carex douglasii*), Kentucky bluegrass (*Poa pratensis*), many-ribbed sedge (*C. multicostata*), meadow barley (*Hordeum brachyantherum*), Nebraska sedge (*C. nebrascensis*), redtop (*Agrostis gigantea*), and tufted hairgrass (*Deschampsia caespitosa*). Common forbs included Chamisso arnica (*Arnica chamissonis*), common dandelion (*Taraxacum officinale*), common yarrow (*Achillea millefolium*), fringed willowherb (*Epilobium ciliatum*), lambstongue ragwort (*Senecio integerrimus*), largeleaf avens (*Geum macrophyllum*), longleaf starwort (*Stellaria longifolia*), pleated gentian (*Gentiana affinis*), slender cinquefoil (*Potentilla gracilis*), thistle (*Cirsium* spp.), and western aster (*Symphyotrichum ascendens*). Black Spring meadow community was assessed to be moderately similar to its potential natural community with 43% of species moderately similar and 28% of species highly similar to the potential natural community (C. Howell, HTNF, personal communication 2001).

Monument Spring

Monument Spring (41º 56.7' N, 115º 14.7' W; 2,094 m elevation; aspect NE; 4.4% slope) is located in the HTNF Spring Creek cattle allotment. Spring Creek allotment (3,083 ha) was managed under a 3-pasture rest rotation grazing system and stocked with cow/calf pairs at a rate of approximately 1.40 AUM/ha from 1 July through 15 October 1999 and 2000. The grazing unit in which Monument Spring was located was grazed both years. The cattle exclosure encompassed 2.5 ha around a spring. A buck and pole fence comprised the northeast exclosure corner. The meadow community at Monument Spring was classified as a dry graminoid/Cryoboroll/trough drainageway ecological type (Weixelman et al. 1996).

Common graminoids included Baltic rush, Kentucky bluegrass, many-ribbed sedge, meadow barley, prairie junegrass (*Koeleria macrantha*), slender wheatgrass (*Elymus trachycaulus*), streambank wheatgrass (*E. lanceolatus*), and timothy (*Phleum pratense*). Common forbs included common yarrow, common dandelion, field pennycress (*Thlaspi arvense*), longleaf starwort, mountain deathcamas (*Zigadenus elegans*), pale agoseris (*Agoseris glauca*), Rocky Mountain iris (*Iris missouriensis*), slender cinquefoil, western aster, and yellow evening-primrose (*Oenothera flava*). Monument Spring meadow community had very low similarity to the potential community with no high similarity species, and 37% and 63% of species, respectively, expressed moderate and low similarity to the potential natural community (C. Jean, HTNF, personal communication 1999).

Sagehen Spring

Sagehen Spring (41º 56.2' N, 115º 0.8' W; 2,017 m elevation; NE aspect; 5.0% slope) is located in the HTNF Wilson Creek cattle allotment. Wilson Creek allotment (2,434 ha) was managed under a 3-pasture deferred rotation grazing system and stocked with cow/calf pairs at a rate of 0.70 AUM/ha from 1 July through 30 September 1999, and 0.66 AUM/ha from 7 July through 30 September 2000. The cattle exclosure encompassed 0.7 ha around a spring. Sagehen Spring meadow community was a mesic graminoid/Aquic Cryoboroll/trough drainageway ecological type (Weixelman et al. 1996).

Common graminoids included Baltic rush, clustered field sedge (*C. praegracilis*), Douglas' sedge, Kentucky bluegrass, Mat muhly (*Muhlenbergia richardsonis*), prairie junegrass, redtop, slender wheatgrass, and tufted hairgrass. Common forbs included Chamisso arnica, common dandelion, Idaho blue-eyed grass (*Sisyrinchium idahoense*), longleaf starwort, Oregon checkerbloom (*Sidalcea oregana*), pleated gentian, Rocky Mountain iris, rosy pussytoes (*Antennaria rosea*), Rydberg's penstemon (*Penstemon rydbergii*), slender cinquefoil, thistle, and western aster. Sagehen Spring meadow community was moderately similar to the potential natural community with 32% of species moderately and 38% of species highly similar to the potential natural community (C. Jean, HTNF, personal communication 1999).

METHODS

Exclosure Experimental Design

Our experimental design was a randomized complete block with repeated measures for 2 years (1999 and 2000) over 3 seasons: (1) before cattle entry (early summer, mid- to late June); (2) peak production (mid-summer, early to mid-August); and (3) end of growing season (fall) production following cattle removal (late September to mid-October). The randomized block with 3 blocks and 3 treatments served as the whole plot and 3 seasons sampled over 2 years were the repeated measures (split plot). Therefore, tests for whole plot factors have fewer degrees of freedom than tests involving time factors. A 3-way grazing exclosure was constructed in each meadow community (blocks) in fall 1998 by adding a woven wire ungulate-proof exclosure to the existing cattle-proof exclosure (Fig. 2). Each 3-way exclosure consisted of an ungulate-proof exclosure (control) and 2 treatments (wildlife use only, and combined cattle and wildlife use; Fig. 2). In fall 1998 we clipped 10 random 0.1-m^2 (20 × 50 cm) quadrats to 5 cm in paired 225-m^2 areas inside and outside the cattle-proof exclosures at Monument and Sagehen Springs to evaluate utilization. We did not consider Black Spring in fall 1998 use estimates as cattle had grazed inside this exclosure. We found mean herbaceous dry matter (DM [g/0.1-m^2]) was 94.0 and 93.2% lower in the combined use area compared to the exclosure (grazed by wildlife only) at Monument and Sagehen Springs, respectively. Tracks and fecal pats indicated use was primarily attributable to cattle, thus we designated the combined use treatment as the cattle treatment.

The woven wire ungulate-proof exclosures, 2.5-m high × 15.3 m × 15.3 m, provided protection from ungulate use within a 234-m^2 area (Fig. 2). A 225-m^2 plot was established within each ungulate exclosure (control). A 225-m^2 plot outside the ungulate-proof exclosure, but inside the cattle exclosure provided access to big game while restricting cattle use (wildlife treatment). A 225-m^2 plot was selected outside the exclosure to evaluate use by cattle and wildlife (cattle treatment). At each sampling occasion, a grid was established in each 225-m^2 plot to facilitate placement of sampling quadrats. Grids consisted of 10 perpendicular lines spaced 1.5 m apart along a 15.24-m center baseline. Ten locations for sampling quadrats were spaced in 1.5 m intervals along each of these lines for a total of 100 possible sampling locations (Fig. 2).

All ANOVAs were analyzed with Statistical Analysis System software (SAS; PROC GLM; SAS Institute 2001). Outlier observations were removed (no more than 2 most extreme to approach balance) if they had a large influence on model variance as detected in residual × predicted plots, and appropriate transformations of treatment responses were conducted if responses did not meet assumptions of statistical tests (Oehlert 2000). Highest order non-significant interaction terms in ANOVA models were pooled into sampling error. Estimated treatment response least squares means were back-transformed (Fowler et al. 1998). Standard errors associated with transformed least squares means were approximated to their original scale according to the delta method (Bishop et al. 1975). Reported treatment estimates were accordingly back-transformed lsmeans ± 1 SE. We conducted post hoc multiple comparisons with Tukey-Kramer HSD tests. Significance was set at $\alpha = 0.05$.

Productivity, Use, and Species Richness of Herbaceous Phytomass

We ocularly estimated standing crop (g) for each species within 15 randomly selected, 0.1-m^2 (20 × 50 cm) sampling quadrats at each 225-m^2-treatment plot during each sampling period. We used double sampling to estimate phytomass by forage class (forbs and graminoids) within 0.1-m^2 quadrats (Bonham 1989). Shrubs were a very minor component and were not considered in analyses. Standing crop of forbs and graminoids (grasses, sedges, and rushes) was estimated in all 15 quadrats and standing crop in 3 quadrats in the wildlife and cattle treatments and 5 quadrats in controls were clipped to ground level and separated and weighed (Interagency Technical Reference 1996). Fresh weights were recorded to the nearest 0.5 g and samples weighing less than 0.5 g (traces) were recorded as 0.1 g.

Linear regressions using estimated fresh weights as independent variables and clipped weights as dependent variables (PROC REG; SAS Institute 2001) by forage class in 0.1-m^2 quadrats at each meadow location in each sampling period were used to calibrate estimates of fresh standing crop in quadrats that were not clipped. Clipped samples were placed in paper bags and initially air-dried to prevent degradation, then oven dried in a forced-air oven at 60 ºC for 24 hours and weighed to ± 0.01 g. Mean % DM from clipped quadrats in the same treatments was multiplied by calibrated estimates of fresh herbage in estimated quadrats to calculate g DM/m^2 for ocularly estimated quadrats. Average g DM/m^2 was calculated at each location from g DM in all 15, 0.1-m^2 quadrats.

We evaluated end of growing season use at each meadow. Total fall herbage (forbs plus graminoids) estimated at each control served as the comparison to total fall herbage estimated in wildlife and cattle treatments. Percent use was thus calculated as the difference in mean g DM/m^2 between the control and each treatment in fall (i.e., % use = [(control g – treatment g)/control g] × 100). Herbaceous species richness in 0.1-m^2 sampling quadrats was pooled in each treatment across seasons and years and was further pooled among the control and wildlife treatment to calculate exclosure richness.

Clipping Treatments Experimental Design

We clipped 5 random 0.1-m^2 quadrats inside big game exclosures in early summer (mid- to late June) and mid-summer (early to mid-August) 1999 and 2000 to simulate light use (mean % fresh clipped weight removed/0.1-m^2 = 13.3–24.7%) on annual production. Elk feeding sites in sagebrush and meadow communities in our study area indicated very light use of perennial forbs (9.1 ± 1.8 %; mean ± 1 SE) and perennial graminoids (1.3 ± 0.3 %; Appendix 2) similar to elk use levels (1.8–13.7%) reported by Hayden-Wing (1979) for total meadow production in central Idaho. Our clipping levels were higher than these elk use levels. In addition, the 5 quadrats previously clipped to ground level in the big game exclosure during early summer and mid-summer 1999 and 2000 to evaluate standing crop were used to compare biomass regrowth following total defoliation. All clipped quadrats were marked with flagged wire to facilitate placement of 0.1-m^2 quadrats in fall.

Our experimental design was a split plot design. The whole plot was a randomized complete block with 3 blocks (exclosures) and 5 treatments: (1) light use in June (early summer light use); (2) clipped to ground in June (early summer total use); (3) light use in August (mid-summer light use); (4) clipped to ground in August (mid-summer total use); and (5) annual production with no use (control). The split plot factor was measurements repeated over 2 years.

We evaluated above ground annual yield (seasonally clipped herbage plus end of growing season herbage; Kowalsky 1964, Kelly 1995) in 0.1-m^2 quadrats clipped in early and mid-summer at light use and total use levels. Yield provided a measure as to whether herbage compensated for defoliation treatments. We compared end of growing season yield (g DM/m^2) in clipped quadrats to annual production in controls. This experimental design was a split plot with randomized complete block whole plot (3 blocks and 5 treatments) and split plot factor being repeated measures over 2 years.

RESULTS

Productivity, Use, and Species Richness of Herbaceous Phytomass

In 1999, we observed use in the wildlife treatments at Black Spring (elk, pronghorn, and greater sage-grouse) and Monument Spring (pronghorn); no wildlife use was detected at Sagehen Spring. We detected elk (Black Spring), pronghorn (Monument Spring), and rabbit (white-tailed jackrabbits and/or mountain cottontail [*Sylvilagus nuttallii*]; Sagehen Spring) use in wildlife treatments in 2000. In 1999 and 2000 we detected cattle use at each meadow location by August. Cattle use was very light (<5%) in mid-summer at some meadows due to grazing allotment rotations, but increased by fall. Cattle use of total herbaceous biomass was higher in 2000 (64.6 ± 24.5%) than in 1999 (42.8 ± 23.2%; Table 1). Mean percent use of total herbaceous biomass after cattle removal in fall in cattle treatments was 2.2-times higher in 1999 and 4.5-times higher in 2000 than in wildlife treatments (Table 1).

Herbaceous species richness was 35 in both the Black Spring exclosure (21 forbs, 9 grasses, 2 rushes, and 3 carices) and in the cattle treatment (18 forbs, 13 grasses, 2 rushes, and 2 carices). The exclosure and cattle treatment both shared 65.7% of the same species (i.e., percentage of species identified in the exclosure and also identified in the cattle treatment and vice versa). Total species list overlap at the Black Spring exclosure and adjacent cattle treatment was 23 of 47 species (48.9%). Monument Spring exclosure herbaceous species richness was 37 (23 forbs, 11 grasses, 1 rush, and 2 carices) and 32 (19 forbs, 9 grasses, 1 rush, and 3 carices) in the cattle treatment. The exclosure shared 62.2% of species found in the cattle treatment, while 71.9% of the species in the cattle treatment were also found in the exclosure. Total species list overlap at the Monument Spring exclosure and adjacent cattle treatment was 23 of 46 species (50.0%). Sagehen Spring herbaceous species richness was 33 (22 forbs, 8 grasses, 1 rush, and 2 carices) in the exclosure and 31 (20 forbs, 7 grasses, 1 rush, and 3 carices) in the cattle treatment. The exclosure shared 78.8% of species found in the cattle treatment, while 83.9% of the species in the cattle treatment were also found in the exclosure. Total species list overlap at the Sagehen Spring exclosure and adjacent cattle treatment was 26 of 38 species (68.4%).

There were no differences in forb standing crop among treatments or between years. There was a significant difference in forb standing crop among seasons ($F_{2,33} = 22.41$, $P < 0.001$). There was less forb biomass in fall than in early summer or mid-summer, but no difference in forb standing crop from early summer to mid-summer across all treatments. Significant differences were detected in forb standing crop for season × year ($F_{2,33} = 14.52$, $P < 0.001$), treatment × year ($F_{2,33} = 5.06$, $P = 0.012$), and treatment × season ($F_{4,33} = 3.90$, $P =$

0.011) interactions. Forb standing crop (mean g DM/m^2) was nearly twice as high in early summer 2000 (37.1 ± 3.7 g) as in early summer 1999 (19.8 ± 2.7 g), but was essentially the same by fall (Fig. 3A). Forb biomass was 59.9% higher in wildlife treatments and 4.6% in controls, but was 39.5% less in cattle treatments from 1999 to 2000 (Table 2). Forbs decreased from early summer through fall in all treatments, but decreased significantly more in cattle treatments (Fig. 3B). Forb standing crop in cattle treatments did not differ from forb standing crop in wildlife treatments in 1999, but was less in 2000 (Table 2).

There was no difference in graminoid standing crop among treatments, seasons, or for the season × year interaction. Mean graminoid standing crop (g DM/m^2) across all treatments was 40.1% higher in 1999 (138.7 ± 12.2) than in 2000 (99.0 ± 8.7; $F_{1,32} = 7.25$, $P = 0.011$). There were significant differences between treatment × year ($F_{2,32} = 3.80$, $P = 0.033$) and treatment × season ($F_{4,32} = 5.00$, $P = 0.003$) interaction terms. Graminoid biomass was 3.1% higher in wildlife treatments, and 21.6 and 55.0% less in controls and cattle treatments, respectively, from 1999 to 2000 (Table 2). From early summer through fall, graminoid standing crop generally increased in controls, increased from early summer to mid-summer and then stabilized through fall in wildlife treatments, and decreased in cattle treatments from mid-summer to fall (Fig. 3C). There were no differences in graminoid standing crop among treatments in 1999, while there was significantly less graminoid biomass in cattle treatments in 2000 than in the control or wildlife treatments (Table 2).

Clipping Treatments

There was a significant difference for forb ($F_{4,8} = 15.56$, $P < 0.001$) and graminoid ($F_{4,8} = 21.78$, $P < 0.001$) g DM/m^2 among clipping treatments. Forb and graminoid production in quadrats lightly clipped in early summer and mid-summer did not differ from

1999 or 2000 control quadrat production (Table 3). Fall graminoid production in quadrats clipped to ground in early summer did not differ from production in quadrats clipped to ground in mid-summer 1999 and 2000, respectively. Yearly forb production in quadrats clipped to ground in mid-summer was significantly less than forbs clipped to ground in early summer (Table 3).

Mean g DM/m^2 was higher across all treatments in 1999 (forbs, 9.4 ± 0.9; graminoids, 113.0 ± 7.3) than in 2000 (forbs, 6.6 ± 0.6; graminoids, 83.3 ± 6.3) for forbs ($F_{1,10} = 6.96$, $P = 0.025$) and graminoids ($F_{1,10} = 9.31$, $P = 0.012$). There was a significant treatment × year interaction for forbs ($F_{4,10} = 10.64$, $P = 0.001$) and graminoids ($F_{4,10} = 3.65$, $P = 0.044$). Forbs and graminoids clipped to ground level in early summer and mid-summer regrew by fall on average (mean for 1999 and 2000) to no more than 19.2, 4.2, 24.7, and 10.0%, respectively, of the amount in control quadrats. Forb and graminoid yield in clipped quadrats did not differ from annual fall g DM/m^2 in control quadrats among treatments or years.

DISCUSSION

Productivity, Use, and Species Richness of Herbaceous Phytomass

Recent work in Montana suggests exclosures need to be larger than 4 ha in size to facilitate equal elk presence inside and adjacent to exclosures (Gross and Knight 2000). Comparisons of elk and cattle use around exclosures could thus be biased, as elk may not be willing to cross fences to access smaller exclosures (Gross and Knight 2000). However, the smallest exclosure (Black Spring, 0.3 ha) was the only exclosure where we documented elk use. Elk in our study appeared to be willing to cross fences to access limited meadow forage.

Fall use in cattle treatments was very high on 3 occasions (Black Spring 1999, 83.6%; Black Spring 2000, 94.5%; Monument Spring 2000, 83.3%). Although 1 April snow water equivalents at the Pole Creek Administrative Site were 470 mm in 1999 and 467 mm in 2000, early summer warming coupled with strong winds and a 49.5 % reduction in June–October cumulative precipitation in 2000 apparently reduced biomass productivity and stimulated earlier phenological development of herbs in communities across the study area. Weather patterns reducing productivity likely contributed to higher cattle use levels in 2000.

Because it is often impossible to enumerate the number of species in a community, we consider the number of species we tabulated for species richness to be an underestimate (Krebs 1999). Forb diversity may increase in areas grazed by cattle in northern Nevada (Clary and Medin 1990); however, we detected 2–4 more forb species in exclosures than in cattle treatments at each meadow community. Graminoid richness comparisons between exclosures and controls were more similar, but showed no consistent patterns. Wildlife and trespass cattle grazing since exclosures were built may have had some effect in increasing or maintaining slightly higher species richness in exclosures. Similarly, Green and Kauffman (1995) found lower richness in dry and wet meadows excluded from grazing for 10 years, compared to the richness of adjacent areas grazed up to 70% in northeastern Oregon. Similarity indices indicate historical grazing in the study area has altered potential vegetation compositions at meadow complexes (Weixelman et al. 1996). Establishment of exotic grasses such as Kentucky bluegrass and timothy at meadow communities in our study area has likely further deflected compositional development away from potential conditions. Therefore, our species richness comparisons probably reflect responses of different portions of meadow communities to grazing and grazing exclusion following historical grazing and introduction of exotics. Overall, species lists overlapped 48.9–68.4% at exclosures and cattle treatments at each meadow. By comparison, species lists overlapped 57.9 ± 2.8% between long-ungrazed and adjacent plots at 26 long-term Rocky Mountain grassland exclosures in Colorado, Montana, South Dakota, and Wyoming (Stohlgren et al. 1999).

Some have reported that relatively moderate grazing can elevate productivity of many types of grasslands above levels in the absence of grazing (McNaughton 1993, Noy-Meir 1993); however, other researchers indicate plant overcompensation in response to grazing on western rangelands rarely occurs (Painter and Belsky 1993). Evidence suggests cattle grazing can facilitate increased levels of graminoid biomass preferentially selected by sympatric cervids (Gordon 1988). Higher production and survival of red deer (*C. elaphus*) has been observed in areas on the Isle of Rhum in Scotland grazed by cattle compared to areas not grazed by cattle (Gordon 1988). Some western mountain grasslands have deteriorated where elk grazing follows cattle grazing, suggesting that compensation either is not sufficient to withstand a second grazing activity (Patten 1993) or that overuse, rather than compensation, occurs. Furthermore, elk may concurrently forage in summer in areas with cattle or forage completely absent from cattle in rested allotments (Werner and Urness 1998, Halstead et al. 2002), suggesting other factors such as habitat selection are more important than cattle grazing in facilitating elk grazing.

Clipping Treatments

Timing of use is important, as elk used forbs and grasses in central Idaho mountain meadows most frequently in July, whereas sedges and rushes were used most in June (Hayden-Wing 1979). Our clipping treatments did not indicate forb or graminoid production was affected by light clipping in early summer or mid-summer. Compensation did not occur following our clipping treatments in northeastern Nevada mountain meadows where growth and regrowth were most likely promoted by subirrigated soils underlying these meadow communities. Clipping mountain meadow vegetation in central Idaho to 5 cm in early June to simulate elk use and then again in late June to simulate cattle use resulted in yields similar to cattle only grazing simulated in late June (Kowalsky 1964). In contrast, clipping to 5 cm in early June yielded results similar to no grazing (Kowalsky 1964). Likewise, biomass of tufted hairgrass clipped to 5 cm to simulate elk use in early June in east central Idaho did not differ from unclipped plants 1 or 2 months after treatment (Kelly 1995). These results suggest that elk use of mountain meadows in early summer has negligible effects on total yearly production of meadow vegetation. However, Kelly (1995) reported yield of tufted hairgrass clipped to simulate elk use in early June and cattle use in early August was lower than clipping treatments to simulate elk use in early June and cattle use in early July.

MANAGEMENT IMPLICATIONS

Timing of grazing on mountain meadow forbs is a critical concern. In our study, forb availability declined throughout summer, especially in cattle treatments, and total use clipping treatments in early and mid-summer resulted in low regrowth of forbs. However, where management is intended to reduce cattle use on riparian areas, cattle stocked in early summer (late June) at moderate rates (average of 2.08 AUM/ha) tend to graze mountain meadows heavier than nearby riparian areas (Clary and Booth 1993).

The location of mountain meadows will play an important role in their probability of use by wild ungulates. Elk used mountain meadows greatest when they were adjacent to cover and secluded from roads and other human activity in northcentral Idaho (Kowalsky 1964). Elk in eastern Arizona demonstrated selection, though not as pronounced as deer, for nearby forest edge over wet meadow and transition areas (Patton and Judd 1970). Infrequent visits to meadows were probably to obtain meadow food plants containing higher protein levels than plants in drier sites (Patton and Judd 1970). Excessive early season use will dramatically decrease annual herbage production. Managers should identify meadows that receive consistent early summer use by elk and then restrict cattle grazing these meadows to late summer or early fall to avoid impairing productivity of graminoids and especially forbs.

LITERATURE CITED

Bishop, Y. M. M., S. E. Fienberg, and D. W. Holland. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, Massachusetts, USA.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, New York, New York, USA.

Clanton, D. C., and D. F. Burzlaff. 1966. Grazing cattle on sub-irrigated meadows. Journal of Range Management 19:151–152.

Clary, W. P., and G. D. Booth. 1993. Early season utilization of mountain meadow riparian pastures. Journal of Range Management 46:493–497.

_____, and D. E. Medin. 1990. Differences in vegetation biomass and structure due to cattle grazing in a northern Nevada riparian ecosystem. U.S. Forest Service Research Paper INT-427.

Cooper, C. S., R. R.Wheeler, and W. A. Sawyer. 1957. Meadow grazing—1: a comparison of gains of calves and yearlings when summering on native flood meadows and sagebrush-bunchgrass range. Journal of Range Management 10:172–174.

Fowler, J., L. Cohen, and P. Jarvis. 1998. Practical statistics for field biology. Second edition. John Wiley & Sons, Chichester, West Sussex, England.

Gomm, F. B. 1979. Grazing management on mountain meadows. Pages 147–163 *in* R. H. Delaney and J. Borrelli, editors. Proceedings of the symposium on management of Intermountain meadows. University of Wyoming College of Agriculture and Colorado State University Mountain Meadow Research Center.

Gordon, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology 25:1–10.

Green, D. M., and J. B. Kauffman. 1995. Succession and livestock grazing in a northeastern Oregon riparian ecosystem. Journal of Range Management 48:307–313.

Gross, J. A., and J. E. Knight. 2000. Elk presence inside various-sized cattle exclosures. Journal of Range Management 53:287–290.

Gruell, G. E. 1998. Northern Elko County: the way it was. Northeastern Nevada Historical Society Quarterly 98-4:105–126.

Hackett, E. I. 1984. Planning a fertilizer program—Nevada suggestions. Pages 81–90 *in* E. G. Siemer and R. H. Delaney, editors. Proceedings of the second Intermountain meadow symposium. Colorado State University and University of Wyoming Agricultural Experiment Stations, Gunnison, Colorado, USA.

Halstead, L. E., L. D. Howery, G. B. Ruyle, P. R. Krausman, and R. J. Steidl. 2002. Elk and cattle forage use under a specialized grazing system. Journal of Range Management 55:360–366.

Hayden-Wing, L. D. 1979. Elk use of mountain meadows in the Idaho primitive area. Pages 40–46 *in* M.S. Boyce and L.D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming, Laramie, Wyoming, USA.

Interagency Technical Reference. 1996. Sampling vegetation attributes. U.S. Forest Service; U.S. Natural Resource Conservation Service: Grazing Land Technology Institute; and, U.S. Bureau of Land Management. U.S. Bureau of Land Management, National Applied Resource Sciences Center, BLM/ST-96/002+1730.

Kelly, S. M. 1995. Elk and cattle range relations on the Lemhi Mountains, Idaho. Thesis, University of Wyoming, Laramie, Wyoming, USA.

Kowalsky, S. I. 1964. Ecology of mountain meadows and use by elk. Thesis, University of Idaho, Moscow, Idaho, USA.

Krebs, C. J. 1999. Ecological methodology, second edition. Benjamin/Cummings, Menlo Park, California, USA.

Loope, L. L. 1969. Subalpine and alpine vegetation of northeastern Nevada. Dissertation, Duke University, Durham, North Carolina, USA.

Manning, M. E., and W. G. Padgett. 1995. Riparian community type classification for Humboldt and Toiyabe national forests, Nevada and eastern California. U.S. Forest Service R4-Ecol-95-01. Intermountain Region, Ogden, Utah, USA.

Mantz, G. K. 1993. Spring elk effects on the availability of summer cattle forage in the Uinta Mountains of Utah. Thesis, Utah State University, Logan, Utah, USA.

McNaughton, S. J. 1993. Grasses and grazers, science and management. Ecological Applications 3:17–20.

Nevada Division of Wildlife. 1997. Nevada elk species management plan. Nevada Division of Wildlife, Reno, Nevada, USA.

Noy-Meir, I. 1993. Compensating growth of grazed plants and its relevance to the use of rangelands. Ecological Applications 3:32–34.

Oehlert, G. W. 2000. A first course in the design and analysis of experiments. W. H. Freeman, New York, New York, USA.

Painter, E. L., and A. J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications 3:2–9.

Patten, D. T. 1993. Herbivore optimization and overcompensation: does native herbivory on western rangelands support these theories? Ecological Applications 3:35–36.

Patton, D. R., and B. I. Judd. 1970. The role of wet meadows as wildlife habitat in the Southwest. Journal of Range Management 23:272–275.

Reid, E. H., and G. D. Pickford. 1946. Judging mountain meadow range condition in eastern Oregon and eastern Washington. U.S. Department of Agriculture Circular 748. U.S. Government Printing Office, Washington, D.C.

SAS Institute. 2001. SAS/STAT User's Guide, Release 8.2. SAS Institute Incorporated, Cary, North Carolina, USA.

Scott, J.M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'erchia, T. C. Edwards, Jr., J. Ulliman, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123.

Stohlgren, T.J., L.D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45–64.

Timothy, K. 1980. Jarbidge Ranger District: it can be done. Rangelands 2:160–161.

U.S. Forest Service. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. U.S. Forest Service, Humboldt National Forest, Elko, Nevada.

Weixelman, D. A., D. C. Zamudio, and K. A. Zamudio. 1996. Central Nevada riparian field guide. U.S. Forest Service, INT-R4-ECOL-96-01. Sparks, Nevada, USA.

Werner, S. J., and P. J. Urness. 1998. Elk forage utilization within rested units of rest-rotation grazing systems. Journal of Range Management 51:14–18.

Young, J. A., and R. A. Evans. 1989. Silver state rangelands—historical perspective. Rangelands 11:199–203.

Table 1. Percent use of total herbaceous biomass (forbs and graminoids) in mountain meadows by cattle and wildlife, Jarbidge Mountains, Nevada, fall 1999 and 2000. Reported are mean differences (± 1 SE%) in g DM/m^2 between controls and cattle and wildlife treatments in fall.

	1999	2000
	(%)	
Cattle	42.8 ± 23.2	64.6 ± 24.5
Wildlife	19.5 ± 1.1	14.4 ± 15.4[a]

[a] This estimate reflects 11.9% more herbage in the wildlife treatment than in the control at Monument Spring in fall 2000.

Table 2. Mountain meadow treatment × year graminoid and forb standing crop (g DM/m^2; lsmeans ± SE), Jarbidge Mountains, Nevada, 1999 and 2000. Standing crop estimates are averaged across seasons and within years.

Treatment	Forbs	Graminoids
	(g DM/m^2)	(g DM/m^2)
1999		
Control	26.2 ± 3.1^{A}	171.4 ± 27.5^{A}
Cattle	18.5 ± 2.8^{AB}	126.0 ± 20.3^{A}
Wildlife	14.2 ± 2.3^{BC}	123.6 ± 19.9^{A}
2000		
Control	27.4 ± 3.2^{A}	134.4 ± 19.9^{A}
Cattle	11.2 ± 2.0^{B}	56.7 ± 9.1^{B}
Wildlife	22.7 ± 2.9^{AC}	127.4 ± 20.5^{A}

^{ABC}Estimates in the same column followed by the same superscript are not different ($P > 0.05$) as tested by Tukey-Kramer HSD tests.

Table 3. Mountain meadow forb and graminoid response (g DM/m^2; lsmeans ± SE) in fall to clipping treatments, Jarbidge Mountains, Nevada, 1999 and 2000.

Treatment	Forbs	Graminoids
	---------------------------- (g DM/m^2)	--------------------------
1999		
Control[a]	24.3 ± 5.2^{A}	167.9 ± 20.2^{A}
Early summer light use[b]	13.2 ± 2.8^{A}	174.8 ± 20.7^{A}
Early summer total use[c]	9.1 ± 1.9^{AC}	80.2 ± 14.0^{AB}
Mid-summer light use	9.9 ± 2.1^{A}	165.5 ± 20.1^{A}
Mid-summer total use	2.6 ± 0.5^{B}	26.6 ± 8.1^{BC}
2000		
Control	27.8 ± 6.0^{A}	172.8 ± 20.5^{A}
Early summer light use	16.5 ± 3.6^{A}	174.0 ± 20.6^{A}
Early summer total use	2.8 ± 0.6^{BC}	16.1 ± 6.3^{C}
Mid-summer light use	19.4 ± 4.2^{A}	147.9 ± 19.0^{A}
Mid-summer total use	0.5 ± 0.1^{D}	9.7 ± 4.9^{C}

[a] Controls were yearly herbage production in unclipped quadrats clipped to ground in fall.

[b] Light use quadrats were clipped to remove 13.3–24.7% of standing herbage at each defoliation event.

[c] Total use quadrats were clipped to ground level.

^{ABCD}Estimates in the same column followed by the same uppercase superscript are not significantly different (*P* > 0.05) as tested by Tukey-Kramer HSD tests.

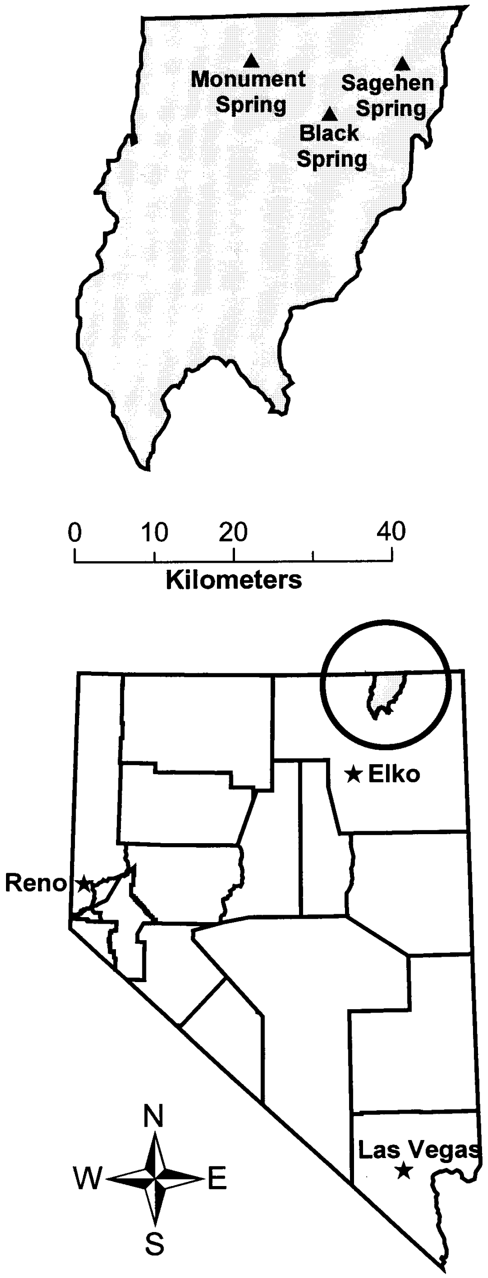


Fig. 1. Location of mountain meadow communities, Jarbidge Mountains, Nevada. The study area encompassed the 166,500 ha Nevada Division of Wildlife Hunt Unit 072. Map projection UTM Zone 11; Datum NAD 1927.

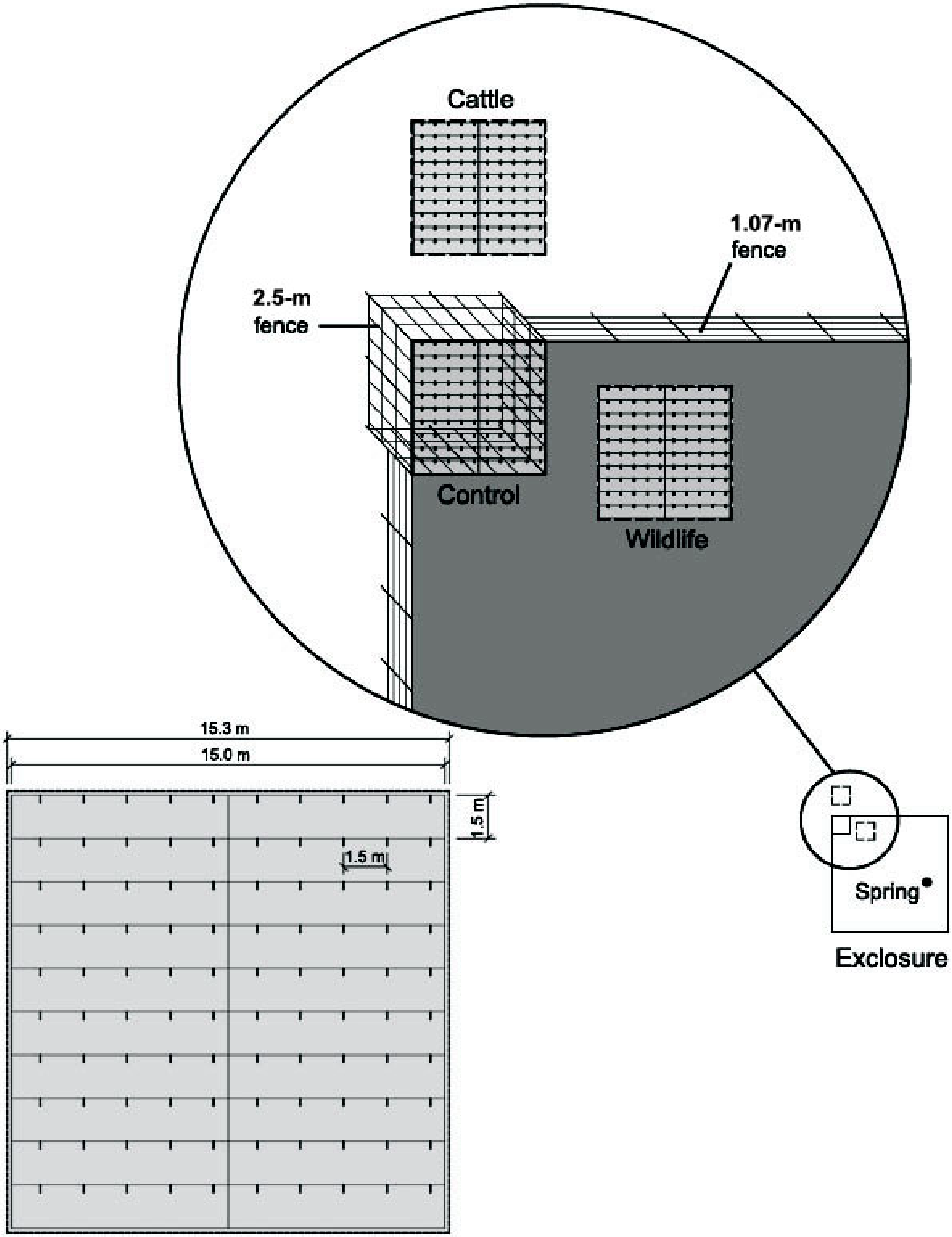


Fig. 2. Mountain meadow exclosure experimental design, Jarbidge Mountains, Nevada. A 2.5-m fence restricted all grazing in controls. A 1.07-m fence allowed access to big game while restricting livestock in wildlife treatments. The cattle treatment was not fenced. A grid consisting of 100 locations for 0.1-m^2 sampling quadrats spaced 1.5 m apart was placed inside a 225.0-m^2 plot at each treatment location.

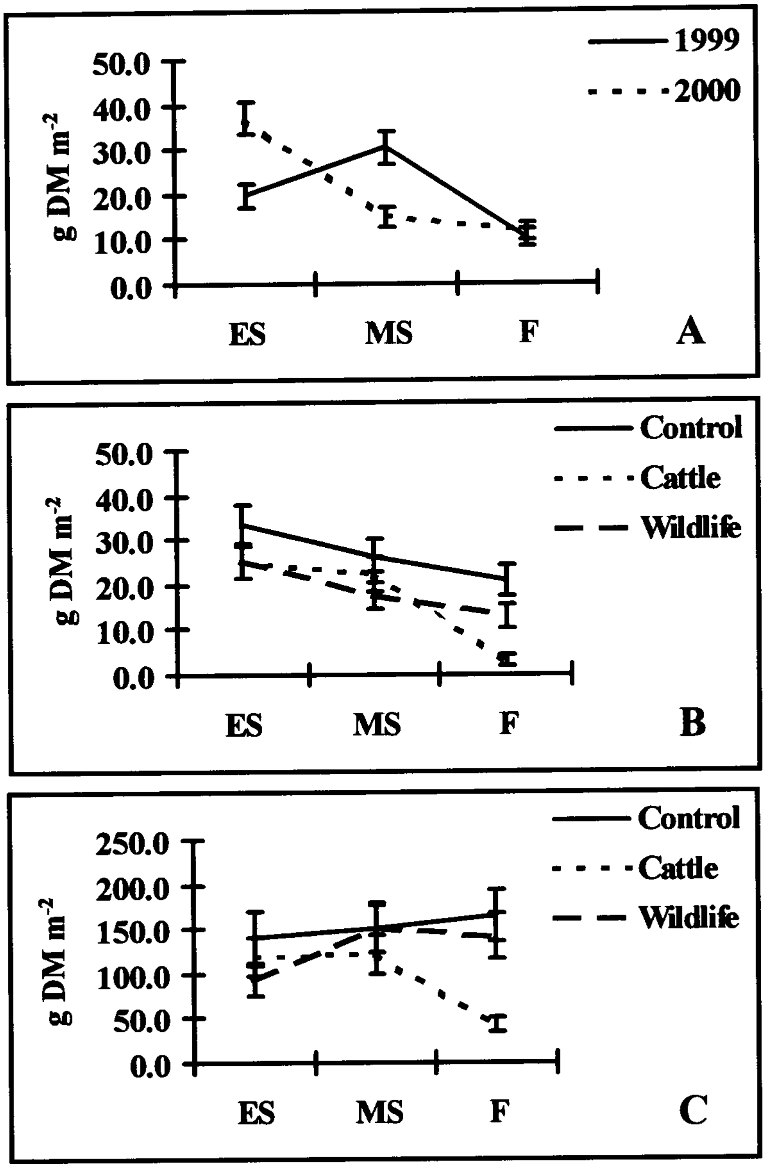


Fig. 3. Mountain meadow standing crop (g DM/m^2; lsmeans ± SE) of (A) forbs, year × season, across all treatments, (B) forbs, treatment × season, across years, and (C) graminoids, treatment × season, across years. Seasons are early summer (ES), mid-summer (MS), and fall (F) and years are 1999 and 2000.

CHAPTER 3

ELK, MULE DEER, CATTLE, AND DOMESTIC SHEEP DIET RELATIONSHIPS ON ARID MONTANE SUMMER RANGE

INTRODUCTION

Dietary patterns and overlap indices for sympatric ungulates provide insights into potential interspecific competition, population nutritional needs, and forage allocation and can be used to identify key indicator plants of rangeland health. Competition for food has been studied more than other aspects of competitive interactions among large herbivores (Miller 2002) even though the relationship between interspecific competition and niche overlap is ambiguous (Abrams 1980). However, the magnitude of diet overlap should indicate potential competition at high population densities.

Morphophysiological characteristics such as salivary glands, body and mouth sizes, type of digestive system (cecal or ruminant), and rumino-reticular volume to body weight ratios predispose ungulates to selectively harvest forages (Hanley 1982, Hanley and Hanley 1982, Hofmann 1989). Advanced forestomach development in cattle and sheep facilitates efficient digestion of graminoids that are high in cell wall, while smaller forestomachs and large salivary glands in deer facilitate nutrient assimilation from heavily defended, nutritious, and highly digestible forbs and woody browse high in cell solubles (Hofmann 1989). Elk (*Cervus elaphus*) are intermediate in digestive capabilities, displaying great variability in seasonal forage selection. Elk forage ranges from highly digestible forbs, woody stems, and young grasses to less digestible coarse forages such as mature grasses and sedges (Cook 2002). Hofmann (1973, 1989) classified ungulates as concentrate selectors or browsers, intermediate feeders, and grazers, while Robbins et al. (1995) and Gordon and Illius (1996) considered feeding categories to be a simple function of body size. Diet selection, including that of range cattle, is influenced by seasonal forage availabilities (e.g., Tueller and Monroe 1975, Ralphs and Pfister 1992, Kie and Boroski 1996).

Several studies have described diets of mule deer (*Odocoileus hemionus*) in Nevada (Pudney 1972 as reported in Papez 1976, Tueller 1979, Spalinger 1980); however, no investigations of elk food habits in the state are available. We compared diets of a recently reintroduced elk population with other ungulates in northeastern Nevada. We hypothesized that elk diets will be proportionately composed of more graminoids and woody browse during dry years when forb abundances are reduced. Our objectives were to: (1) investigate elk, mule deer, cattle, and domestic sheep diet composition on shared northeastern Nevada summer range over 3 years, (2) describe food niche overlap among this suite of ungulates, and (3) identify potentially competitive foraging scenarios for these herbivores on shared, arid montane summer ranges.

STUDY AREA

Summer range (≥2,135 m) covers about 48% of our 166,500 ha study area (41º 30' to 42º 00' N–115º 00' to 115º 30' W) in the Jarbidge Mountains of northeastern Nevada. The Humboldt-Toiyabe National Forest comprises 94,226 ha (56.6%), Bureau of Land Management 35.9%, and private lands 7.5 % of the study area. Elevations range from 1,633 to 3,287 m. The northern slope of the Jarbidge Mountains drains into the Snake River, while southern watersheds feed into the Great Basin (U.S. Forest Service 1981). Moisture arrives mainly as snow. Snow water equivalents at Draw Creek (2,300 m) and Pole Creek Ranger Station (2,540 m) Natural Resource Conservation Service Snowtel sites were 126, 88, and 104% and 94, 91, and 90%, of 30-yr averages in 1998, 1999, and 2000, respectively. Mean monthly temperatures (ºC) averaged from June through October, 1998, 1999, and 2000 were 12.1 ± 2.5, 11.3 ± 2.1, and 13.6 ± 2.0 at Draw Creek, and 10.1 ± 2.7, 9.6 ± 2.4, and 11.4 ± 2.0 at Pole Creek. June through October cumulative precipitation (mm) was 135 and 229 in 1998, 104 and 102 in 1999, and 41 and 51 in 2000 at Draw Creek and Pole Creek Ranger Station, respectively.

Mountain big sagebrush (*Artemisia tridentata vaseyana*) and low sagebrush (*A. arbuscula*) interspersed with meadows form a matrix between forested communities. Forested communities include aspen (*Populus tremuloides*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), snowbrush (*Ceanothus velutinus*), and conifer including subalpine fir (*Abies lasiocarpa*), and limber (*Pinus flexilis*) and whitebark pines (*Pinus albicaulis*). Lewis (1975) described herbaceous species in each community.

Elk were reintroduced into the Jarbidge Mountains from 1990–95 (Nevada Division of Wildlife 1997) and a population of about 300 (summer range density = 0.4/km^2) was maintained by antlerless harvest from 1996–2000 (Chapter 1). Elk share summer range with mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), cattle, and domestic sheep. Mule deer densities averaged 7.9/km^2 from 1998 to 2000 in the study area (L. Gilberston, Nevada Department of Wildlife, personal communication 2003). Livestock graze 11 sheep, 27 cattle, and 1 common use summer and early fall allotments.

METHODS

Fecal Collections

It was important to properly identify the species for each fecal collection because elk and mule deer were sympatric with each other and with cattle and domestic sheep in summer. Summer fecal samples were collected at 1–3 week intervals from 10 July until mid-September, 1998–2000. Samples were collected from single defecations to maintain sample integrity. Feces were only collected from adults to remove bias associated with milk ingested by juveniles.

Elk spring diet samples were collected from late-May through 9 July before summer livestock grazing. Samples from adult elk in groups consisting of cows, calves, and yearling bulls were collected in summer to compare to those of female cattle and sheep. Radiocollared elk cows were located from fixed-wing flights, relocated on the ground, and then focal animals were selected for sampling to represent group locations (Altmann 1974, Chapter 5). Some additional fecal samples from groups with no collars were also included. Spring elk pellets represented female and male groups. Pellets were collected from 2 defecations from single elk groups in those instances when herds were scattered across a larger area in 2 or more communities (Irwin and Peek 1983). Each elk collection consisted of at least 12 individual pellets from single elk fecal deposits.

We located cattle groups in the Black Spring/Caudle Creek, and Pole Creek allotments, and domestic sheep groups in the Elk Mountain and Raker Creek allotments in the north of the study area to increase sampling efficiency. Livestock stocking rates, area, and composition of the 5 major cover types for each allotment are reported in Table 1. During sampling periods we rotated searches between allotments to locate livestock groups to collect fecal samples because livestock were regularly herded among units in each allotment. Frequent consulting with herders provided information on whereabouts of livestock. Individual cattle and sheep were randomly selected to represent center of group locations via focal animal sampling (Altmann 1974). A sample was collected from only 1 fresh cattle pat at each cattle group location. Three-to-five pellet groups were collected from groups of sheep to represent dietary diversity inherent within bands. Multiple focal animals or focal group centers were randomly selected to collect fecal collections from large sheep groups. Elk, cattle, and sheep fecal samples were collected within 1 week of group locations to ensure freshness. Fresh mule deer pellets were collected from the northern portion of the study area with freshness based on color and consistency. We searched areas frequented by mule deer for fresh fecal samples because we did not have any radio-collared deer to provide locations. In addition, we collected fecal samples from several deer we observed defecating.

Fresh feces were salted (NaCl), oven-dried at 90-100 ºC for at least 1 hr, and placed in a closed box containing a breathable canister of naphthalene to prohibit fungal and insect infestations (Litvaitis et al. 1994). Four g from each cattle pat, 5 g from each individual summer elk collection, and 6 pellets, or equivalent fecal matter, from each individual spring elk, mule deer, and sheep collection were combined to form composite diet samples by species, season (elk only), and year. Composite fecal samples provide accurate results while reducing costs and improving sampling efficiency compared to individual sample analysis (Jenks et al. 1989, Gogan and Barrett 1995).

Microhistological Fecal Analysis

Composite fecal samples were submitted for microhistological analysis to the Wildlife Habitat and Nutrition Laboratory, Washington State University (Pullman, Washington, USA). Lists of potential forage species and voucher specimens collected throughout the study area were provided to lab workers to aid in identification of plant fragments in fecal samples. Diets were analyzed as percent cover (Korfhage 1974, Davitt 1979) of plant fragments by species or genera at 100X magnification of 25 randomly placed microscope views on each of 8 slides. Larger magnification (200X to 450X) was used to aid in identification of discernable plant fragments (Holechek and Valdez 1985). Percent diet composition was calculated by dividing cover of each plant species or genera by total cover observed for all species and multiplying by 100.

The digestion residue of in vitro forage, weighed in proportion to the diet composition results obtained, provided correction factors to adjust for differential digestibility (Pulliam and Nelson 1979, Smitman 1980). Epidermal and cuticular fragments in the in vitro residue were analyzed for relative cover as outlined above. Correction factors represented forage class level (forbs, graminoids, browse) with 100 views. Final dietary fractions thus represented the product of forage class correction factors with the original dietary percentage for each species.

Statistical Analyses

We transformed dietary proportions to account for the unit sum constraint (i.e., data sum to 1) inherent in compositional data. Forbs, graminoids, and browse in each diet were transformed into 2 dependent variables by relating natural log ratios of proportions of forbs to browse (ln[forbs/browse]) and proportions of graminoids to browse (ln[graminoids/browse]) in each diet (Aebischer et al. 1993). We designated browse as the denominator in these ratios because browse formed the smallest portion of each diet, thus facilitating a better understanding of the relative contribution of forbs and graminoids to each diet. The above ratios were assessed to see if they met the assumptions of multivariate analysis of variance (MANOVA) including multivariate normality and covariance homogeneity. Statistical procedures were conducted with Statistical Analysis System software (SAS; SAS Institute 2001). Statistical significance was set at $\alpha = 0.05$.

We used MANOVA to evaluate the effect of year and species on use of forage ratios. It was impossible to assess the interaction of year and species due to the lack of replication (i.e., only 1 diet × species × year), so we conducted Tukey's one-degree-of-freedom tests on both dependent variables to fit an additive model to evaluate whether there was a significant year × species interaction. Tukey one-degree-of-freedom tests facilitate transformation of dependent variables if significant interactions are present to improve linear models by removing interactions when MANOVA null hypotheses are rejected (Oehlert 2000).

We used canonical variates analysis to identify the dimensionality of the alternative hypothesis (Johnson 1998). Because there was no significant year effect we conducted a univariate analysis with the first canonical variate as the dependent variable and year and species as independent variables. We thus pooled data over the 3 years and plotted species least squares means (ln[graminoids/browse] by ln[forbs/browse]) to depict the separation of group means (elk in spring, and elk, mule deer, cattle, and domestic sheep in summer) in 2-dimensional space. Tukey-Kramer's multiple comparisons on estimates of the first canonical variate facilitated detecting which species diet group means differed.

We examined the importance of common forage species in ungulate diets because they may be useful indicators of rangeland productivity. Forbs were arrowleaf balsamroot (*Balsamorhiza sagittata*) and spurred lupine (*Lupinus caudatus*); grasses were bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), Kentucky bluegrass (*Poa pratensis*), mountain brome (*Bromus marginatus*), needlegrasses (*Achnatherum* spp.), and Sandberg bluegrass (*Poa secunda*); and woody species were aspen, curlleaf mountain mahogany (hereafter, mountain mahogany), mountain snowberry (*Symphoricarpos oreophilus*), and snowbrush ceanothus.

We computed dietary overlap as the sum percent overlap of forage plants common to each pair of ungulate species diets, with overlap ranging from 0 to 100% (Schoener 1970, Gogan and Barrett 1995). Schoener's index is not restricted by assumptions of competition, does not change when non-utilized resources are considered, and is not sensitive to subdivision of resource states by researchers (Abrams 1980). Spearman's rank correlations (Proc CORR; SAS Institute 2001) examined relationships between percentages of plants in diets among ungulate pairs.

RESULTS

Elk largely ate forbs (about 60%) in summer, while elk spring diets were more variable (Fig. 1). Mule deer diets for all 3 summers were composed of about 30% browse and 67% forbs, and 1.6–5.3% graminoids. Cattle diets were dominated by graminoids (≥91.5%) over all summers (Table 2; Fig. 1). Sheep diets consisted of little browse (0.1–5.2%), about 70% graminoids and 23% forbs in 1998 and 1999, and then decreased to 42.0% graminoids and increased to 57.9% forbs in 2000 (Fig. 1). Rank order of mean species richness in diets from 1998 to 2000 was spring elk (34) > summer elk (29.7) > mule deer (27.7) > sheep (24) > cattle (21; Table 2). Lupines (*Lupinus* spp.) formed ≥11.3% of elk, deer, and sheep diets over all summers (Table 2). Twelve forage species accounted for 44.2 to 85.3% of all diets, and 6 grass species contributed 52.4 to 81.6% to cattle diets and 38.4 to 58.3% to sheep diets (Table 2).

Residual by predicted plots and normal quantile plots for each dependent variable revealed that the sheep 2000 diet had a large influence on covariance homogeneity and multivariate normality and was thus not considered in the MANOVA. We detected a difference in diet composition among species (Wilk's $\Lambda = 0.02$, $F_{8,12} = 8.45$, $P = 0.001$), but not in diet composition between years (Wilk's $\Lambda = 0.51$, $F_{4,12} = 1.22$, $P = 0.355$). Ratios of graminoids to browse were highest in cattle (5.4 ± 0.8; least squares mean ± SE) and domestic sheep (2.9 ± 1.0) diets. Mule deer selected the lowest ratio of graminoids to browse (-2.3 ± 0.8; Figs. 1, 2). Diets of mule deer in summer (0.9 ± 0.4) and elk in spring (0.5 ± 0.4) composed a lower natural log ratio of forbs to browse than cattle (2.1 ± 0.4), domestic sheep (1.8 ± 0.5), or elk in summer (1.6 ± 0.4; Fig. 2).

The canonical variates likelihood ratio test for year was not significant ($P = 0.355$), whereas the canonical variates likelihood ratio test for species indicated the dimensionality of the alternative hypothesis was 1 as only the first canonical variate was significant ($P = 0.001$). In addition, cumulative variation (92.3%) for the eigenvalue of the first canonical variate indicated species groups fell along a line further indicating that only 1 canonical variate was required to separate species groups. Group means differed ($P = 0.001–0.045$) between all diet pairs, except elk in spring with sheep, elk in summer with mule deer and sheep, and cattle with sheep (Table 3).

Highest dietary overlap was between cattle and domestic sheep (40.4–68.1%, r_s = 0.66–0.71, $P < 0.001$), and lowest overlap was between mule deer and cattle (2.8–7.9%, $P > 0.05$). Elk and deer diets moderately overlapped in summer with the highest overlap in 1998 (59.0%; $r_s = 0.39$, $n = 60$, $P < 0.01$; Table 4). Sheep diets were moderately similar to elk diets in spring (30.6–42.2%), and summer (22.1–64.5%), and spring elk diets were somewhat similar (13.8–45.7%) to summer cattle diets (Table 4).

DISCUSSION

A potential weakness of composite samples is a loss of sample variability compared to individual samples. However, there were no statistical differences in composite diets over 3 summers, a relationship that has been found to be similar to testing data from individual diet sample averages (Jenks et al. 1989). Percentages of forage classes in cattle and mule deer diets remained static, whereas elk and sheep demonstrated greater flexibility in yearly diets. Warm, windy weather in late spring and early summer 2000 limited growth and hastened maturity of herbaceous forage (Appendix 2). Although we did not detect a significant difference among years, elk apparently selected rapidly maturing forbs in spring over graminoids, while sheep ate more forbs and less graminoids and browse during summer 2000 than in 1998 or 1999. Although it is unclear why spring elk and summer sheep forage selection in 2000 changed from preceding years, both ungulates demonstrated plasticity in diet selection in response to foraging conditions.

We identified 3 species of lupine in the Jarbidge Mountains: rolled (*L. lepidus aridus*), spurred (*L. caudatus*), and sulphur (*L. sulphureus*). Spurred lupine was the most abundant lupine on summer range and was frequently eaten by elk and domestic sheep at feeding sites; rolled and sulphur lupine were not actively eaten by foraging ungulates, and sulphur lupine tended to be distributed at lower elevations. Although species level identification of lupines in microhistological analysis was not possible, feeding site evidence indicates spurred lupine was the dominant lupine selected by ungulates. Spurred lupine contains potentially poisonous alkaloids and has been reported to cause cattle deaths (Kingsbury 1964). Some lupines are valuable or highly valuable elk forage, while many have limited forage value for elk (Cook 2002). Spurred lupine in the Jarbidge Mountains maintains crude protein through early fall and digestible energy through mid-summer at levels exceeding lactating cow elk requirements (Chapter 4).

High browse and low grass proportions, and large forb components, where available, have characterized food habits of mule deer on Nevada summer range (Pudney 1972 as reported in Papez 1976, Tueller 1979, Spalinger 1980). However, rumen analysis from 4 Nevada summer ranges in one study revealed lupines composed <1.0% of deer diets (Tueller 1979). Nutritional benefits of spurred lupine in our study area may have exceeded deleterious effects, if any, from alkaloids. Mule deer may rely heavily on 1 or 2 species when other forages lack adequate protein in late summer (Austin and Urness 1985), and herd productivity in 2 southeastern Utah mule deer populations was related to differences in quantity and quality of forbs on summer range (Pederson and Harper 1978). Lupine use in our study may likewise be related to nutritional benefits lacking in other forage sources.

There were reportedly 560,000 domestic sheep as well as cattle and horses grazing the Jarbidge and nearby Independence and Gold Creek Ranger Districts in 1908 (Gruell 1998). Historical and excessive cattle herbivory caused ranges to be dominated by forbs and high sheep grazing pressure created ranges composed largely of grasses on the Wasatch

Plateau in central Utah (Ellison 1954). Consequently, we believe historically high levels of sheep grazing in the Jarbidge Mountains have influenced composition and productivity in many communities, particularly for forbs. Current diet patterns probably reflect past livestock grazing influences, particularly by large groups of domestic sheep.

Conditions that must exist for forage competition among ungulates include: (1) species use the same area, (2) forage plants must be in short supply or are impaired in production due to combined use, and (3) species use the same forage plants (Cole 1958:27, Holechek 1980:158). Our dietary data indicate that certain foraging situations among ungulates on Nevada mountain summer ranges could lead to competition. Cattle and sheep grazing on the same allotment at the same time would be especially inappropriate given their high degree of dietary overlap. A potential conflict could arise between increasing elk populations and mule deer during summer owing to the magnitude of diet overlap between these cervids. We would predict higher diet overlap in summer among elk, sheep, and mule deer in dry years, when forb nutrients and availabilities are reduced. By comparison, diet overlap between tule elk (*C. e. nannodes*) and black-tailed deer (*O. h. columbianus*) in northern California was highest during dry summer months when fecal nitrogen was lowest and both species simultaneously selected forbs (Gogan and Barrett 1995). Similarly, pronghorn and livestock dietary overlap was greatest in north-central New Mexico during a dry year when forage availability was reduced (Stephenson et al. 1985).

MANAGEMENT IMPLICATIONS

Increasing elk populations may or may not negatively affect populations of other ungulates on common summer range. A large array of environmental factors and their interactions could all influence population growth and productivity of other ungulates including use of previously unoccupied range, resource partitioning, and even potential changes in plant community productivity and nutrition (Singer and Norland 1994). Nevertheless, our study indicates forbs are a fundamental component of elk, mule deer, and domestic sheep diets, thus managers must maintain high diversity and abundance of plants on shared Great Basin summer ranges (Timothy 1980). Efforts to reduce forbs or browse to increase grass forage would negatively affect foraging opportunities for most ungulates.

Increasing elk populations could elevate diet overlap with mule deer and sheep, and possibly cattle, and lead to competitive interactions. Elk may have the greatest flexibility of any North American ungulate to select food items in grassland and shrubland forest environments (Hanley and Hanley 1982). Future monitoring of the 12 dietary species we report is critical because they are common rangeland species and changes in composition of these plants should be useful to indicate trends in rangeland health. In particular, arrowleaf balsamroot, spurred lupine, bluebunch wheatgrass, mountain brome, needlegrasses, mountain mahogany, and snowbrush ceanothus, should be monitored due to their importance in elk diets. Monitoring productivity and use of key forage species and foraging areas should compliment future elk population objectives.

LITERATURE CITED

Abrams, P. 1980. Some comments on measuring niche overlap. Ecology 61:44–49.

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Austin, D. D., and P. J. Urness. 1985. Values of four communities for mule deer on ranges with limited summer habitat. Journal of Range Management 38:167–171.

Cole, G. F. 1958. Big game-livestock competition on Montana's mountain rangelands. Montana Wildlife (Apr):24–30.

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

Davitt, B. B. 1979. Elk summer diet composition and quality on the Colockum Multiple Use Research Unit, central Washington. M.S. Thesis, Washington State University, Pullman, Washington, USA.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecological Monographs 24:89–184.

Gogan, P. J. P., and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. Journal of Range Management 48:327–335.

Gordon, I. J., and A. W. Illius. 1996. The nutritional ecology of African ruminants: a reinterpretation. Journal of Animal Ecology 65:18–28.

Gruell, G. E. 1998. Northern Elko County: the way it was. Northeastern Nevada Historical Society Quarterly 98-4:105–126.

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

_____, and K. A. Hanley. 1982. Food resource partitioning by sympatric ungulates on Great Basin rangeland. Journal of Range Management 35:152–158.

Hofmann, R. R. 1973. The ruminant stomach: stomach structure and feeding habits of East African game ruminants. East African Monographs in Biology, volume 2. East African Literature Bureau, Nairobi, Kenya.

_____. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443–457.

Holechek, J. L. 1980. Concepts concerning forage allocation to livestock and big game. Rangelands 2:158–159.

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

Irwin, L. L., and J. M. Peek. 1983. Elk, *Cervus elaphus*, foraging related to forest management and succession in Idaho. Canadian Field-Naturalist 97:443–447.

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.

Johnson, D. E. 1998. Applied multivariate methods for data analysts. Duxbury Press, Pacific Grove, California, USA.

Kie, J. G., and B. B. Boroski. 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. Journal of Range Management 49:482–488.

Kingsbury, J. M. 1964. Poisonous plants of the United States and Canada. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Korfhage, R. C. 1974. Summer food habits of elk in the Blue Mountains of northeastern Oregon based on fecal analysis. M.S. Thesis, Washington State University, Pullman, Washington, USA.

Lewis, M. E. 1975. Plant communities of the Jarbidge Mountain complex, Humboldt National Forest. Report to Intermountain Region, U.S. Forest Service, Ogden, Utah, USA.

Litvaitis, J. A., K. Titus, and E. M. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and foods. Pages 254–274 *in* T.A. Bookhout, editor. Research and management techniques for wildlife and habitats, fifth edition. The Wildlife Society, Bethesda, Maryland, 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, second edition. Smithsonian Institution Press, Washington, D.C.

Nevada Division of Wildlife. 1997. Nevada elk species management plan. Nevada Division of Wildlife, Reno, Nevada, USA.

Oehlert, G. W. 2000. A first course in the design and analysis of experiments. W. H. Freeman, New York, New York, USA.

Papez, N. J. 1976. The Ruby-Butte deer herd. Project W–48–R–6, Biological Bulletin 5. Nevada Department of Fish and Game, Reno, Nevada, USA.

Pederson, J. C., and K. T. Harper. 1978. Factors influencing productivity of two mule herds in Utah. Journal of Range Management 31:105–110.

Pudney, R. A. 1972. Food preference of mule deer on the Ruby-Butte study area. Thesis, University of Nevada, Reno, Reno, Nevada, USA

Pulliam, D. E., Jr., and J. R. Nelson. 1978. Determination of digestibility coefficients for quantification of fecal analysis with elk. Pages 240–246 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming, Laramie, Wyoming, USA.

Ralphs, M. H., and J. A. Pfister. 1992. Cattle diets in tall forb communities on mountain rangelands. Journal of Range Management 45:534–537.

Robbins, C. T., D. E. Spalinger, and W. van Hoven. 1995. Adaptation of ruminants to browse and grass diets: are anatomical-based browser interpretations valid? Oecologia 103:208–213.

SAS Institute. 2001. SAS/STAT User's Guide, Release 8.2. SAS Institute, Incorporated, Cary, North Carolina, USA.

Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

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.

Smitman, G. E. 1980. An examination of laboratory techniques for quantification of elk fecal analysis. Thesis, Washington State University, Pullman, Washington, USA.

Spalinger, D. E. 1980. Mule deer habitat evaluation based upon nutritional modeling. Thesis, University of Nevada, Reno, Nevada, USA.

Stephenson, T. E., J. L. Holechek, and C. B. Kuykendall. 1985. Drought effect on pronghorn and other ungulate diets. Journal of Wildlife Management 49:146–151.

Timothy, K. 1980. Jarbidge Ranger District: it can be done. Rangelands 2:160–161.

Tueller, P. T. 1979. Food habits and nutrition of mule deer on Nevada ranges. Project W-48-5, Study I, Job 2, University of Nevada Agricultural Experiment Station. Reno, Nevada, USA.

_____, and L. A. Monroe. 1975. Management guidelines for selected deer habitats in Nevada. Publication Number R 104, University of Nevada Agricultural Experiment Station. Reno, Nevada, USA.

U.S. Forest Service. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. U.S. Forest Service Humboldt National Forest, Elko, Nevada, USA.

Table 1. Area (ha), mean stocking rate (AUM[a]/ha ± SE), and composition (%) of cover types in allotments where livestock fecal samples were collected, Jarbidge Mountains, Nevada, 1998–2000. Summer range cover compositions provided for comparison.

Allotment	Area	Stocking rate	Composition (%)				
	(ha)	(AUM/ha)	Aspen	Conifer	Mahogany	Sagebrush– herb	Snowbrush
Cattle							
Black/Caudle	5,271	0.79 ± 0.03	8.5	0.1	6.1	83.0	2.3
Pole Creek	3,174	0.55 ± 0.05	10.9	7.3	10.9	69.0	1.9
Spring Creek	3,083	1.43 ± 0.03	6.3	3.5	10.0	79.1	1.1
Domestic sheep							
Elk Mountain	2,977	0.34 ± 0.00	22.4	5.1	27.9	42.8	1.8
Raker Creek	4,710	0.25 ± 0.00	13.7	22.6	21.8	40.0	1.9
Summer range	80,159		15.1	10.7	19.7	51.8	2.7

[a] AUM = animal unit months, or forage demand for 1 animal unit for 30 days.

Table 2. Elk, mule deer, cattle, and domestic sheep diet composition (%) for 12 common forage species, Jarbidge Mountains, Nevada, 1998–2000. Richness is the number of food items in each diet discernable to species or genera. Samples (*n*) are the number of pellet or pat samples included in each seasonal composite diet.

	Diet composition (%)														
	Elk spring			Elk summer			Mule deer			Cattle			Domestic sheep		
	98	99	00	98	99	00	98	99	00	98	99	00	98	99	00
Forbs															
Arrowleaf balsamroot	2.7	0.3	6.6	3.9	1.0	0.1	2.9	1.3	4.3	0.0	0.0	0.0	0.0	0.0	0.0
Lupines	2.5	5.5	17.0	40.5	28.8	38.2	48.2	31.9	43.5	0.4	2.2	0.2	11.3	13.6	46.9
Grasses															
Bluebunch wheatgrass	7.4	7.6	1.6	1.2	4.6	5.4	1.6	0.0	0.0	14.1	20.3	27.0	15.3	11.8	11.5
Idaho fescue	4.3	1.5	1.0	0.0	6.8	5.1	0.6	0.0	0.3	5.3	4.0	3.3	5.7	4.3	1.6
Kentucky bluegrass	0.0	0.0	2.8	1.5	0.0	5.7	0.0	0.0	0.9	3.0	9.4	20.1	5.9	8.3	11.5
Mountain brome	8.9	7.4	1.5	0.6	0.9	2.5	0.1	0.3	0.3	5.0	4.8	2.7	3.5	2.5	0.7
Needlegrasses	6.1	1.5	2.4	0.5	2.6	5.7	0.0	0.6	0.1	18.4	12.7	15.5	15.3	11.7	6.8
Sandberg bluegrass	10.1	7.2	0.0	0.0	6.1	0.0	1.4	0.5	0.0	6.6	10.9	13.0	12.6	16.0	6.3
Woody browse															
Aspen	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mountain mahogany	2.2	7.2	5.4	1.7	0.0	0.0	7.7	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Mountain snowberry	0.8	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Snowbrush ceanothus	5.5	21.6	5.9	1.4	3.8	0.0	4.4	11.6	9.1	0.0	0.0	0.0	0.0	0.8	0.0
Total (%)	50.9	61.3	44.2	51.3	54.6	62.7	66.9	46.6	59.3	53.2	64.3	81.8	69.6	69.0	85.3
Richness	32	32	38	29	31	29	26	28	29	21	26	16	25	30	17
Samples (*n*)	25	11	15	22	20	23	15	27	32	26	29	37	31	64	85

Table 3. *P*-values between elk, mule deer, cattle, and domestic sheep diet group means, Jarbidge Mountains, Nevada, 1998–2000. Differences assessed with MANOVA through Tukey-Kramer multiple comparisons of the first canonical variate. Means were averaged across years and are plotted in Fig. 2. Group means differ when $P \leq 0.05$.

	P-values			
Diet	Elk spring	Elk summer	Mule deer	Cattle
Elk spring				
Elk summer	0.045			
Mule deer	0.003	0.189		
Cattle	0.034	0.001	0.001	
Domestic sheep	0.997	0.053	0.004	0.094

Table 4. Dietary overlap calculated as sum percentage of dietary species common to each ungulate pair (Schoener 1970). Spearman's rank correlations (r_S) examined relationships between percentages of plants in diet pairs, Jarbidge Mountains, Nevada, 1998–2000.

Comparisons	1998[a]		1999[b]		2000[c]	
	Overlap (%)	r_s	Overlap (%)	r_s	Overlap (%)	r_s
Elk spring – Elk summer	17.8	0.18	33.1	0.16	38.7	0.25
Elk spring – Mule deer	24.7	0.45**	31.5	0.25	46.0	0.31*
Elk spring – Cattle	45.7	0.34**	37.0	0.45**	13.8	0.20
Elk spring – Sheep	42.2	0.36**	37.0	0.33*	30.6	0.20
Elk summer – Mule deer	59.0	0.39**	45.2	0.01	49.7	0.16
Elk summer – Cattle	5.9	-0.08	30.1	0.19	25.9	0.39**
Elk summer – Sheep	22.1	0.15	42.9	0.37**	64.5	0.55***
Mule deer – Cattle	6.0	0.05	7.9	-0.14	2.8	-0.08
Mule deer – Sheep	19.9	0.17	24.1	-0.02	49.7	0.10
Cattle – Sheep	58.6	0.71***	68.1	0.70***	40.4	0.66***

[a] Pairwise food items compared (*n*) were 59 for spring elk and 60 for all other diets.

[b] Pairwise food items compared (*n*) were 53 for all diets.

[c] Pairwise food items compared (*n*) were 55 for all diets.

*$P < 0.05$

**$P < 0.01$

***$P < 0.001$

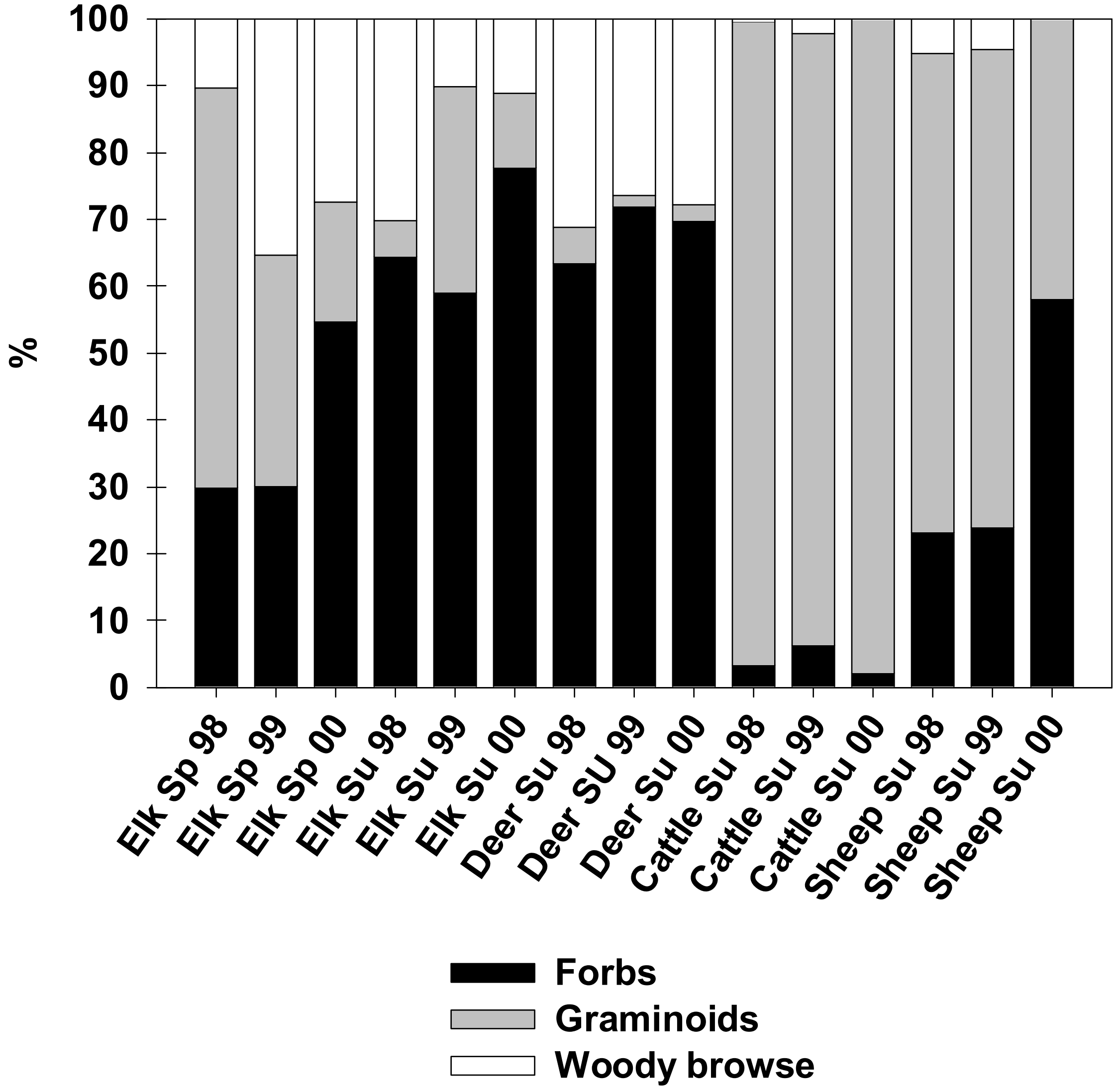


Fig. 1. Composition (%) of forbs, graminoids, and woody browse in elk, mule deer, cattle, and domestic sheep diets, Jarbidge Mountains, Nevada, 1998–2000. Diets were determined through microhistological fecal analysis. Seasons are spring (Sp; late May through 9 July) and summer (SU; 10 July through mid-September). Spring elk diet samples include cow-only and mixed-sex elk groups. Forbs may include small amounts of moss, lichens, or unidentified seeds. Forbs in 2000 elk spring diets include 0.5% insect remains.

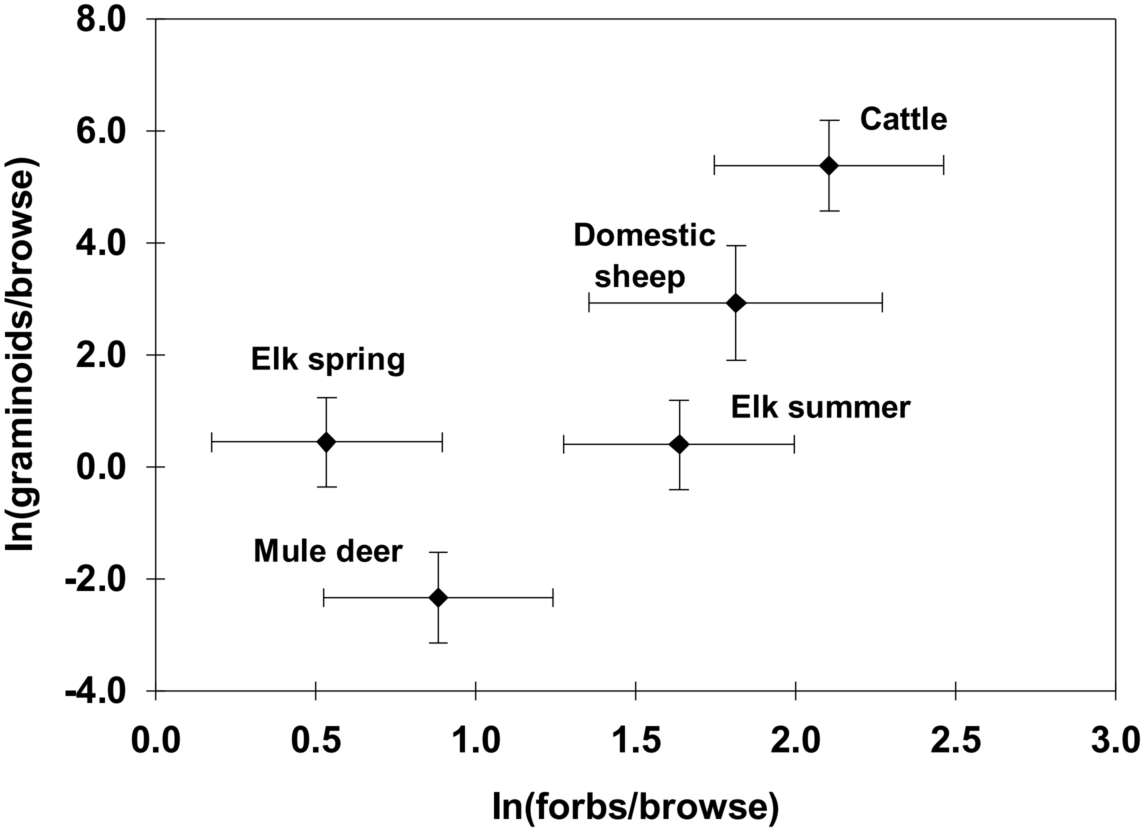


Fig. 2. Least squares means for ungulate diet groups plotted in 2-dimensional space. Group means were averaged over 1998–2000 and are presented as diamonds. Mean (± SE) natural log ratios of graminoids to browse (ln[graminoids/browse]) plotted on the y-axis and mean natural log ratios of forbs to browse (ln[forbs/browse]) plotted on the x-axis. Natural log ratio transformations of dietary composition data removed the linear restriction of data that sum to 1.

CHAPTER 4

NUTRIENT EVALUATION FOR ELK FORAGES ON NORTHEASTERN NEVADA SUMMER RANGE

INTRODUCTION

Elk (*Cervus elaphus*) winter survival can be dependent on body reserves anabolized during summer and autumn and thus depends on forage quality and quantity available while on summer ranges (Mautz 1978, Baker and Hobbs 1982). Recent work suggests elk populations with low pregnancy rates for prime-age females with calves are probably indicative of summer–autumn ranges with depauperate nutrient supplies (Cook et al. 2001). However, high elk pregnancy rates do not necessarily reflect adequate nutritional conditions. Despite high pregnancy rates, adult females on nutritionally marginal summer–autumn ranges may delay breeding and parturition, growth of calves and yearlings may be reduced, and yearling breeding may be lowered (Cook et al. in press). Energetic needs of lactating cow elk in summer are 2 or 3 times higher than during gestation (Robbins 1993), thus foraging options have implications for elk population productivity (Wisdom and Cook 2000). Summer range carrying capacity evaluations must accordingly consider nutrient supplies in key forage plants as limiting nutrients limit population growth.

Although protein, vitamins, energy, fatty acids, water, and micro- and macrominerals are all essential, most wildlife nutritionists agree energy and protein are likely the most limiting nutrients to wildlife populations (Spalinger 2000). Phosphorous, energy, and protein have been found to be limiting to mule deer (*Odocoileus hemionus*) on some Nevada summer ranges, but are sufficient to sustain productive populations on other ranges (Tueller 1979, Spalinger 1980). It has been postulated that expanding elk populations in Nevada will ultimately not be limited by forage conditions (Nevada Division of Wildlife 1997); however, evaluations of forage abundance and quality as related to nutritional needs for elk populations in the state are lacking. Moreover, understanding the relative ability of forages to meet the needs of prime-age females, the productive component of elk populations, is necessary to decipher reasons for declines and potential for population growth (Alldredge et al. 2002). Our nutritional evaluation adds important information to the limited literature on elk–nutrient dynamics for western montane summer ranges. More specifically, our results provide information for elk inhabiting mountain summer ranges where the growth of communities common to this latitude such as aspen (*Populus tremuloides*) is greatly restricted by temperature and moisture (Mueggler 1988). We hypothesize that mid-summer and early fall forage nutrient levels on arid western mountain ranges relegate lactating cow elk to select diets that diverge from the contention that elk are primarily grass grazers.

We selected a cow elk with calf at side lactating through mid-Autumn and with average dry matter intake, activity, and metabolic demands as our model to compare crude protein (CP), digestible energy (DE), and macromineral requirements in summer (Alldredge et al. 2002, Cook 2002). Because we address requirements for plant nutrient levels and not animal nutrient intake, our comparisons apply to lactating cow elk of all body weights. Specific objectives were to (1) estimate seasonal CP, DE, and macromineral levels in common elk summer forage species, (2) evaluate whether forage plant nutrient levels met optimal, seasonal lactating cow elk requirements across summers, and (3) discuss our findings and provide management implications in relation to elk population growth.

STUDY AREA

Our study area comprised Nevada Division of Wildlife (NDOW) Hunt Unit 072 (41º 30' to 42º 00' N and 115º 00' to 115º 30' W) in northeastern Nevada. Hunt Unit 072 consisted of 166,500 ha with elevations ranging from 1,633 to 3,287 m. We delineated all area ≥2,135 m as elk summer range because 91.3% of cow elk groups relocated on radiotelemetry flights across summers 1998–2001 were found in this region. Summer range included 48.1%, or 80,159 ha of the study area, and is administered by Forest Service (91.5%), Bureau of Land Management (5.4%), and private ownership (3.1%). The 39,197 ha Jarbidge Wilderness Area comprised most of the Jarbidge Mountains and 48.9% of the summer range. Northern slopes drain into the Snake River, while southern slopes drain into the Great Basin (USDA Forest Service 1981).

Snowpack provides most moisture. Snow water equivalents on 1 April at 2 Natural Resource Conservation Service SNOTEL sites, Draw Creek (2,300 m) in the south, and Pole Creek Ranger Station (2,540 m) in the north, were 88 and 104%, and 91 and 90%, of 30-yr (1971–2000) averages in 1999 and 2000, respectively. Mean monthly temperatures (ºC) averaged from June through October were 11.3 ± 2.1 in 1999 and 13.6 ± 2.0 in 2000 at Draw Creek, and 9.6 ± 2.4 in 1999 and 11.4 ± 2.0 in 2000 at Pole Creek. June through October 1999 and 2000 cumulative precipitation was 104 and 41 mm at Draw Creek, and 102 and 51 mm at Pole Creek Ranger Station.

Dominant summer range communities were a sagebrush–herb complex composed of mountain big sagebrush (*Artemisia tridentata vaseyana*) and low sagebrush (*A. arbuscula*) interspersed with herbaceous meadows and snowbank associations, aspen, curlleaf mountain mahogany (*Cercocarpus ledifolius*), snowbrush ceanothus (*Ceanothus velutinus*), and a conifer complex including subalpine fir (*Abies lasiocarpa*), and limber (*Pinus flexilis*) and whitebark (*P. albicaulis*) pines. Mountain snowberry (*Symphoricarpos oreophilus*) was widespread in all 5 major communities. Sandberg bluegrass (*Poa secunda*) and Idaho fescue (*Festuca idahoensis*) typically only grew in the sagebrush–herb community association. Needlegrasses (*Achnatherum* spp.) were commonly found in aspen, mahogany, and sagebrush–herb communities. Arrowleaf balsamroot (*Balsamorhiza sagittata*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) inhabited mahogany and sagebrush–herb communities. Mountain brome (*Bromus marginatus*) and Kentucky bluegrass (*P. pratensis*) were common aspen community grasses. Mountain brome was an infrequent component of sagebrush-herb communities and Kentucky bluegrass was a major component of herbaceous meadows in the sagebrush–herb community complex. Spurred lupine (*Lupinus caudatus*) inhabited aspen, mahogany, and sagebrush–herb communities, although greatest productivity was in the sagebrush–herb type (Jensen et al. 1988). Lewis (1975) provided detailed lists of herbaceous species in each community.

Elk were reintroduced into the Jarbidge Mountains from 1990–95 (Nevada Division of Wildlife 1997) and a population of about 300 (summer range density = 0.4/km^2) was maintained by antlerless harvest from 1996–2000 (Chapter 1). Elk share summer range with mule deer, pronghorn (*Antilocapra americana*), cattle, and domestic sheep. Calves per 100 cow ratios from 1 July to mid-September 1998–2000 averaged 52 (range = 32–57; Chapter

1), suggesting a productive, growing elk population with a younger adult female age structure (Wisdom and Cook 2000). Geometric mean finite rates of increase (λ) were 1.08 during the antlerless hunting period (1995–1999) and increased to 1.15 following release from hunting (2000–2003), further indicating productivity of this population under current habitat and management conditions (Chapter 1). New population objectives call for elk to increase to 1,000 ± 100 by 2010, at which time objectives will be reevaluated (Nevada Division of Wildlife 2000).

METHODS

Forage Collections

We collected species that were commonly observed selected by elk at feeding sites and in diets in the study area (Chapter 3). Forbs collected were arrowleaf balsamroot and spurred lupine. Grasses included bluebunch wheatgrass, Idaho fescue, Kentucky bluegrass, mountain brome, needlegrass, and Sandberg bluegrass. Woody browse included aspen, mountain mahogany, mountain snowberry, and snowbrush ceanothus. Forage samples were collected from the Black Spring, Spring Creek, and Wilson Creek cow/calf grazing allotments during early summer (late June), mid-summer (early August), and early fall (late September) 1999 and 2000. Black Spring was managed with Caudle Creek allotment (5,271 ha) as a deferred rotation grazing system with a stocking rate of 0.82 animal unit months (AUM)/ha from 6 July through 11 October 1999 and 0.72 AUM/ha from 1 July through 16 September 2000. Spring Creek allotment (3,083 ha) was managed under a 3-pasture rest rotation grazing system with a stocking rate of approximately 1.40 AUM/ha from 1 July through 15 October 1999 and 2000. Wilson Creek allotment (2,434 ha) was managed under a 3-pasture deferred rotation grazing system with a stocking rate of 0.70 AUM/ha from 1 July through 30 September 1999 and 0.66 AUM/ha from 7 July through 30 September 2000.

We initiated forage collections in each allotment within the same 2-week period in each month over both years. We clipped segments of ungrazed plants to mimic portions of plants we observed eaten by elk at feeding sites; this typically included the inflorescence and basal leaves in forbs and grasses and succulent shoots and current annual growth (CAG) in shrubs. At each forage collection we clipped fresh material and removed old growth to form ≥30 g samples from multiple plants to account for variation among plants. A higher number of plants were clipped from small stature plants such as Sandberg bluegrass and Idaho fescue due to lower availability of standing material. Samples were air-dried in paper bags to prevent fungal growth and later dried in a forced-air oven at 60 ºC. Oven-dried samples were ground to 2 mm in a Wiley Mill and stored in plastic bags at room temperature prior to in-vitro-dry-matter-digestibility (IVDMD), gross energy (GE), and macromineral analyses.

Forage Quality Compositional Analyses

The University of Idaho, Analytical Sciences Laboratory, conducted organic and macromineral compositional analyses. Total carbon (C), nitrogen (N), and sulfur (S) were determined following McGeehan and Naylor's (1988) combustion technique. Concentrations (µg/g) of calcium (Ca), potassium (K), magnesium (Mg), phosphorous (P), and sodium (Na) were determined by inductively coupled plasma - atomic emission spectroscopy (Anderson 1996). Percent crude protein was approximated as 6.25 x [%N] (Robbins 1993). All Na samples were below detectable levels in 2000; therefore, we only report 1999 Na values above detectable levels.

Apparent IVDMD’s were determined according to Pearson (1970) and Tilley and Terry (1963). Rumen inoculum was collected from fistulated beef cows maintained on a diet of approximately 1/3 alfalfa (*Medicago sativa*) and 2/3 grass hays. Dacron filter bags (Ankom Technology, Macedon, New York, USA) were used to contain material during fermentation and all digestion trials were terminated after 48 hr. Triplicates of each species by location and time period were digested to obtain mean percentage IVDMD with CV ≤ 5.0%. Additional replications were conducted until at least 2 replicates could be averaged with an accompanying CV ≤ 5.0%. June and August IVDMD estimates were increased by 11 and 6%, respectively, to correct for underestimation related to air-drying forages that occurs at these time periods (Cook 1990). Gross energy was determined with bomb calorimetry for duplicate composite forb, grass, and woody browse samples representing each allotment and time period; CV for gross energy duplicates were all ≤ 3.2%. Digestible energy (kcal/kg) was approximated as the product of mean apparent IVDMD for each species sample and mean GE for each corresponding forage class by location and time period (Robbins 1993).

Statistical Analyses

Our experimental design was a randomized complete block with repeated measures over 3 seasons and 2 years. The randomized block with 3 allotments (blocks) and 12 species (treatments) served as the whole plot and 3 seasons sampled over 2 years were the repeated measures (split plot). Therefore, tests for whole plot factors have fewer degrees of freedom than tests involving time factors. We used Akaike’s information criterion (AIC) to determine whether autoregressive, autoregressive moving average, compound symmetric, or heterogeneous autoregressive time series covariance structures best fit our data; the covariance structure with the lowest AIC value was selected (Burnham and Anderson 1998).

We pooled seasonal DE and CP responses over both years after finding no seasonal differences within species between years (Tukey-Kramer HSD, $P > 0.05$). Species, season, and the species × season interaction were fixed effects, while allotment and the allotment × season interaction were random effects in our model. Assumptions and tests for all ANOVAs were analyzed with Statistical Analysis System software (SAS; PROC MIXED; SAS Institute 2001). Outlier observations were removed if they had a large influence on model variance as detected in residual x predicted plots. Removing outliers had no effect on ANOVA statistical significance. Crude protein treatment responses were transformed with the arcsine square root transformation, and DE treatment responses were natural log transformed to further meet assumptions of statistical tests (Oehlert 2000).

Because our analyses did not reveal any patterns for macrominerals we report mean ranges in minerals for each forage species across seasons and years. Ranges in minerals were qualitatively compared to gestation and early lactation requirements for beef cattle (National Research Council 1984, 1996). Role of minerals in domestic ruminant nutrition is well understood (Kincaid 1988, Robbins 1993, Van Soest 1994) and required levels are often used as surrogates for elk and other wild ruminants (Cook 2002).

There was no significant allotment × species interaction ($P > 0.05$) for CP or DE, which allowed me to average species responses over allotments. We constructed 95% confidence intervals around raw CP and DE means (PROC MEANS; SAS Institute 2001) and we used 1-tailed, 1-sample *t*-tests (PROC TTEST; SAS Institute 2001) to evaluate whether seasonal CP and DE raw estimates were lower than levels required to provide optimal nutritional status for lactating cow elk in summer (Cook et al. In Press). Optimal performance levels are those that assure animals experience no, or virtually no, limitations from nutrition. Post hoc multiple comparisons were conducted with the Tukey-Kramer HSD test to separate means when significant main effects or interactions were detected. We used Spearman's rank correlations (SAS Proc CORR; SAS Institute 2001) to examine relationships between percentages of the 12 forage plants in spring and summer diets and CP and DE levels in early summer (compared to spring elk diets), mid-summer (compared to summer elk diets), and fall (compared to summer elk diets) 1999 and 2000. Statistical significance was set at $\alpha = 0.05$.

RESULTS

We collected 105 and 108 forage samples in 1999 and 2000, respectively. Aspen was not collected in early summer 1999.

Crude Protein

We detected significant differences ($P < 0.001$) in CP concentrations among species ($F_{11, 22} = 30.47$), season ($F_{2, 152} = 417.13$), and the species × season interaction ($F_{22, 152} = 417.13$). Crude protein decreased in all species across seasons (Table 1). Idaho fescue and Sandberg bluegrass CP levels were below lactating cow elk optimal performance levels in all seasons, while spurred lupine and snowbrush ceanothus CP levels exceeded optimal levels in all seasons (Table 1). Herbaceous CP levels generally exceeded optimal performance in early summer and declined below optimal elk levels in mid-summer and early fall. However, by mid-summer, CP in all grasses was below cow elk optimal levels. Highest CP was spurred lupine in early summer (22.7 ± 4.7%) and lowest was bluebunch wheatgrass in early fall (4.0 ± 1.0%). Mahogany, mountain snowberry, snowbrush ceanothus, spurred lupine, and Kentucky bluegrass all maintained levels above lactating cow elk optimal performance in early fall (Table 1). The spring 2000 elk diet correlated with early summer 2000 CP levels was the only significant diet and CP correlation ($r_s = 0.77$, $n = 12$, $P = 0.004$).

Digestible Energy

We detected significant differences ($P < 0.001$) in DE concentrations among species ($F_{11,\,22} = 17.95$), season ($F_{2,\,149} = 141.22$), and the species × season interaction ($F_{22,\,149} = 8.77$). Digestible energy in all forbs and grasses declined from early summer to early fall. Sandberg bluegrass was the only species that maintained DE below optimal performance levels in all seasons. Three woody browse species, but not curlleaf mountain mahogany in mid-summer, maintained DE levels above lactating cow elk optimal performance levels from early summer through early fall (Table 2). Arrowleaf balsamroot, spurred lupine, and mountain brome DE levels satisfied cow elk optimal levels in mid-summer, but no herbaceous forage met 2,750 kcal/kg DE optimal performance levels in early fall (Table 2). There were no significant correlations between 1999 and 2000 elk diets and DE.

Macrominerals

Mineral concentrations varied widely among species, with no predictable patterns found among allotments, species, seasons, or years. Sodium levels in all forages were below requirements during all time periods. Highest Na level was 62 μg/g, well below the 600 μg/g minimum Na requirement (Table 3). Ranges in S in Sandberg bluegrass and curlleaf mountain mahogany were also below requirements; however, upper mean ranges in Sandberg bluegrass (1,467 µg/g) and curlleaf mountain mahogany (1,400 µg/g) approached 1,500-µg/g requirements (Table 3). Range in all other minerals in all other plants exceeded minimum requirements (Table 3). In many instances low mineral concentrations in plants exceeded upper animal requirement levels; for instance, low Ca, K, and Mg concentrations in arrowleaf balsamroot and spurred lupine exceeded upper range in beef cattle requirements (Table 3). High Ca concentrations in arrowleaf balsamroot and spurred lupine, K in arrowleaf balsamroot and mountain brome, and Mg in spurred lupine exceeded maximum tolerable levels (Table 3).

DISCUSSION

During early growth stages, herbaceous forages typically provide adequate nutrients for growth, to improve body condition, and to promote milk production (Cook 1972, Vallentine 1990). Protein in forbs and grasses typically is initially less than or equal to shrubs, decreases more rapidly, and then typically reaches levels below shrubs by the end of the growing season. Digestible energy tends to be higher in herbaceous plants as compared to shrubs across all stages of growth (Cook 1972). In our study woody browse generally contained highest levels of DE and CP by mid-summer and grasses generally declined in forage quality more rapidly than forbs and woody browse. Mountain snowberry contained markedly higher DE in early summer relative to any other species or season; this was attributable to high mean (± SE) IVDMD of 74.6 ± 1.2% and 70.7 ± 1.2% in 1999 and 2000, respectively. Our findings agree with Dietz (1972) who reported IVDMD for common snowberry (*S. albus*) was 71.4%, the highest of 6 species, during the spring early leaf stage in the Black Hills of South Dakota.

Cow elk groups in our study ate more graminoids in spring and early summer and then switched to a diet dominated by forbs in mid- to late summers (Chapter 3). However, reliance on grasses in spring and summer 1999 coincided with protein and energy levels in bluebunch wheatgrass, Kentucky bluegrass, mountain brome, and needlegrasses that exceeded cow elk optimal levels. Moreover, lupines (*L.* spp.) constituted the major forb consumed, and snowbrush was the major woody plant consumed in mid- to late summers 1998–2000 (Chapter 3), the 2 forage species with the most reliable nutrient supplies across summers. Dietary data provide some evidence that cow elk in our study area demonstrated a functional response to nutrient levels by foraging on seasonally rich nutrient sources. Forage quality in grasses in the Great Basin rapidly declines when abundant moisture promotes phenology that in turn creates numerous reproductive stems (Ganskopp and Bohnert 2001). However, summer precipitation following dry springs may greatly extend the length of time grass nutrients in the region meet animal requirements (Ganskopp and Bohnert 2001). Consequently, variation in annual precipitation can greatly influence plant nutrients and thus ungulate foraging patterns on Great Basin summer range.

Sodium content in forages in our study was at best about 10% of requirements (National Research Council 1996). Ganskopp and Bohnert (2003) found a similar ratio of sodium relative to beef cattle requirements in 7 Great Basin grasses and Alldredge et al. (2002) found average Na content in forages used by elk in northern Idaho was 10% or less of beef cattle requirements. As a rule Na, other than in halophytes, is physiologically not needed by plants and thus does not provide concentrations that meet animal requirements

(Kincaid 1988, Robbins 1993, Van Soest 1994). The ubiquitous drive for salt in spring among herbivores, exacerbated by gestation and lactational needs, results from greater ingestion of seasonally succulent forages that also contain elevated levels of K (Robbins 1993, Van Soest 1994). Grazing animals in spring and summer compensate for low Na by visiting mineral springs, mineral licks, and livestock salt placements to ingest salty water and salt-impregnated soils (Bechtold 1996, Beck et al. 1996). The attractiveness of salty soils surrounding livestock salt placements to wild ungulates is understandable as trace mineralized livestock salt supplements may contain as much as 93–98% NaCl (Beck et al. 1996). Adequate and tolerable macromineral levels were widely available in most forage plants we evaluated. It seems unlikely that elk in the Jarbidge Mountains will suffer mineral deficiencies or toxicities leading to nutritional problems such as grass tetany. In addition, elk in our study had access to at least 400 species of vascular plants (Lewis 1975), providing a wide range of foraging options to obtain adequate minerals and other nutrients.

MANAGEMENT IMPLICATIONS

Future increases in elk populations in the area should be complimented with monitoring plans to ensure key foraging communities and forage species are maintained and/or enhanced. Monitoring should be coupled with hunting seasons to reduce elk populations to prevent overuse of key woody communities. Because 60% (3/5) of the main community structural species, aspen, curlleaf mountain mahogany, and snowbrush ceanothus are nutritious foods, their reproduction, growth, and vigor should be monitored. Overbrowsing these woody plants will reduce the ability of northeastern Nevada summer ranges to provide nutritious forage to meet the demanding requirements of lactating cow elk and their calves.

Sodium sources are greatly lacking in forages on most summer ranges. Elk, deer, pronghorn and other herbivores are thus attracted in spring and summer to dig and eat soil around livestock salt placements. Managers must take into account the effects of this form of geophagia on localized areas. Placement locations therefore should either consider whether fixed salting sites should be used each year or whether placements should be moved yearly to avoid creating pits that wild ungulates repeatedly visit to acquire salt.

Declining forage quality across summer–autumn indicates that elk are increasingly challenged to satisfy optimal nutritional performance levels as the biomass of total forage that meets optimal nutritional performance wanes. Thus, by early fall, foraging options that satisfy requirements are appreciably reduced. It is unclear the extent to which quality of elk diets decline as overall forage quality declines, but it is clear that the potential for maintaining a relatively high density of elk at dietary quality levels that fulfill optimal performance requirements declines as summer progresses. Maintaining highly productive elk herds in northeastern Nevada requires that managers (1) prevent substantial increases in elk population size and (2) maintain those communities that best provide for the nutritional needs of lactating cows and their growing calves.

LITERATURE CITED

Alldredge, M. W., J. M. Peek, and W. A. Wall. 2002. Nutritional quality of forages used by elk in northern Idaho. Journal of Range Management 55:253–259.

Anderson, K. A. 1996. Micro-digestion and ICP-AES analysis for the determination of macro and micro elements in plant tissues. Atomic Spectroscopy 1:30–33.

Baker, D. L., and N. T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. Journal of Wildlife Management 46:694–703.

Bechtold. J. P. 1996. Chemical characterization of natural mineral springs in northern British Columbia, Canada. Wildlife Society Bulletin 24:649–654.

Beck, J. L., J. T. Flinders, D. R. Nelson, C. L. Clyde, H. D. Smith, and P. J. Hardin. 1996. Elk and domestic sheep interactions in a north-central Utah aspen ecosystem. U.S. Forest Service Research Paper INT-RP-491.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information–theoretic approach. Springer-Verlag, New York, New York, USA.

Cook, C. W. 1972. Comparative nutritive values of forbs, grasses, and shrubs. Pages 303–310 *in* C. M. McKell, J. P. Blaisdell, and J. R. Goodin, editors. Wildland shrubs—their biology and utilization. U.S. Forest Service General Technical Report INT-1.

Cook, J. G. 1990. Habitat, nutrition, and population ecology of two transplanted bighorn sheep populations in southcentral Wyoming. Doctoral Thesis, University of Wyoming, Laramie, Wyoming, USA.

_____. 2002. Nutrition and food habits. Pages 259–349 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management, second edition. Smithsonian Institution Press, Washington, D.C.

_____, B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. In Press. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs.

Cook, R. C., D. L. Murray, J. G. Cook, P. Zager, and S. L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology 79:845–853.

Dietz, D. R. 1972. Nutritive value of shrubs. Pages 289–302 *in* C. M. McKell, J. P. Blaisdell, and J. R. Goodin, editors. Wildland shrubs—their biology and utilization. U.S. Forest Service General Technical Report INT-1.

Ganskopp, D., and D. Bohnert. 2001. Nutritional dynamics of 7 northern Great Basin grasses. Journal of Range Management 54:640–647.

_____, and _____. 2003. Mineral concentration dynamics among 7 northern Great Basin grasses. Journal of Range Management 56:174–184.

Jensen, M. E., L. S. Peck, and M. V. Wilson. 1988. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. Great Basin Naturalist 48:403–421.

Kincaid, R. 1988. Macro elements for ruminants. Pages 326–341 *in* D.C. Church, editor. The ruminant animal: digestive physiology and nutrition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Lewis, M. E. 1975. Plant communities of the Jarbidge Mountain complex, Humboldt National Forest. Report to Intermountain Region, U.S. Forest Service, Ogden, Utah.

Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88–90.

McGeehan, S. L., and D. V. Naylor. 1988. Automated instrumental analysis of carbon and nitrogen in plant and soil samples. Communications in Soil Science and Plant Analysis 19:493–505.

Mueggler, W. F. 1988. Aspen community types in the Intermountain Region. U.S. Forest Service General Technical Report INT-250.

National Research Council. 1984. Nutrient requirements of beef cattle. Sixth edition. National Academy Press, Washington, D.C., USA.

_____. 1996. Nutrient requirements of beef cattle, update 2000. Seventh revised edition, National Academy Press, Washington, D.C., USA.

Nevada Division of Wildlife. 1997. Nevada elk species management plan. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2000. Sub-plan for elk management in the Jarbidge Mountains, Nevada. Nevada Division of Wildlife, Reno, Nevada, USA.

Oehlert, G. W. 2000. A first course in the design and analysis of experiments. W. H. Freeman, New York, New York, USA.

Pearson, H. A. 1970. Digestibility trials: in vitro techniques. Pages 85–92 *in* H. A. Paulsen, Jr., E. H. Reid, and K. W. Parker, editors. Range and wildlife habitat evaluation: a research symposium. U.S. Forest Service Miscellaneous Publication 1147.

Robbins, C.T. 1993. Wildlife feeding and nutrition, second edition. Academic Press, San Diego, California, USA.

SAS Institute. 2001. SAS/STAT User's Guide, Release 8.2. SAS Institute Incorporated, Cary, North Carolina, USA.

Spalinger, D. E. 1980. Mule deer habitat evaluation based upon nutritional modeling. Thesis, University of Nevada, Reno, Nevada, USA.

_____. 2000. Nutritional ecology. Pages 108–139 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Tilley, J. M. A., and R. A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. Journal of the British Grassland Society 18:104–111.

Tueller, P. T. 1979. Food habits and nutrition of mule deer on Nevada ranges. Project W-48-5, Study I, Job 2. University of Nevada Agricultural Experiment Station, Reno, Nevada, USA.

U.S. Forest Service. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. U.S. Forest Service, Humboldt National Forest, Elko, Nevada.

Vallentine, J. F. 1990. Grazing management. Academic Press, San Diego, California, USA.

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

Wisdom, M. J., and J. G. Cook. 2000. North American elk. Pages 694–735 *in* S. Demarais, and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Table 1. Seasonal crude protein (% ± 95% CI) in 12 elk forage species, Jarbidge Mountains, Nevada, 1999 and 2000. Values were pooled (*n* = 6) because there were no seasonal differences across years. Estimates compared to optimal performance for lactating cow elk.

Species	Early summer	Mid-summer	Early fall
	-------------------------------	(%)	-------------------------------
Forbs			
Arrowleaf balsamroot	16.7 ± 1.6^{A}	7.6 ± 1.5^{B}*	5.6 ± 1.7^{B}*
Spurred lupine	22.7 ± 4.7^{A}	17.4 ± 3.4^{B}	9.8 ± 1.7^{C}
Grasses			
Bluebunch wheatgrass	14.9 ± 2.8^{A}	7.6 ± 1.6^{B}*	4.0 ± 1.0^{C}*
Idaho fescue	11.6 ± 1.2[a]^{A}*	7.0 ± 1.2^{B}*	5.6 ± 1.2^{B}*
Kentucky bluegrass	15.4 ± 1.7^{A}	10.4 ± 1.1^{B}*	7.7 ± 0.5^{B}
Mountain brome	19.5 ± 5.7^{A}	10.2 ± 1.3^{B}*	6.3 ± 1.6^{C}*
Needlegrass	15.3 ± 2.9^{A}	9.9 ± 2.6^{B}*	4.4 ± 0.8^{C}*
Sandberg bluegrass	7.7 ± 1.4^{A}*	6.7 ± 2.0^{A}*	5.8 ± 1.4^{A}*
Woody browse			
Aspen	13.4 ± 3.2[b]^{A}	12.2 ± 1.1^{A}	5.9 ± 1.1^{B}*
Curlleaf mountain mahogany	13.1 ± 3.6^{A}	9.6 ± 0.7^{A}*	9.0 ± 1.1^{A}
Mountain snowberry	14.9 ± 3.2^{A}	9.4 ± 1.6^{B}*	6.7 ± 1.8^{B}
Snowbrush ceanothus	17.0 ± 3.4^{A}	12.7 ± 0.3^{B}	9.7 ± 0.5^{B}
Optimal performance[c]	14	12	8

[a] Outlier removed (*n* = 5).

[b] June 2000 aspen only (*n* = 3).

[c] Optimal performance levels are those that assure animals experience no, or virtually no, limitations from nutrition. Crude protein optimal performance levels from Cook (2002).

^{ABC}Means in the same row followed by the same uppercase superscript are not different ($P > 0.05$) as tested by Tukey-Kramer HSD tests.

*Estimate less than optimal performance ($P < 0.05$) as tested by 1-tailed, 1-sample *t*-test.

Table 2. Seasonal digestible energy (kcal/kg ± 95% CI) in 12 elk forage species, Jarbidge Mountains, Nevada, 1999 and 2000. Values were pooled (*n* = 6) because there were no seasonal differences across years. Estimates compared to optimal performance for lactating cow elk.

Species	Early summer	Mid-summer	Early fall
	----------------------------	(kcal/kg)	---------------------------
Forbs			
Arrowleaf balsamroot	3,479 ± 177^{A}	2,777 ± 300^{B}	2,294 ± 310^{aB}*
Spurred lupine	3,498 ± 220^{A}	2,767 ± 431^{B}	2,416 ± 116^{B}*
Grasses			
Bluebunch wheatgrass	2,892 ± 234^{A}	2,311 ± 374^{B}*	2,181 ± 346^{aB}*
Idaho fescue	2,716 ± 373^{A}	2,372 ± 495^{A}*	2,176 ± 503^{aA}*
Kentucky bluegrass	3,027 ± 102^{A}	2,291 ± 310^{B}*	2,166 ± 281^{B}*
Mountain brome	3,447 ± 221^{A}	2,822 ± 197^{A}	2,229 ± 134^{B}*
Needlegrass	2,969 ± 167^{A}	2,146 ± 303^{B}*	1,746 ± 210^{B}*
Sandberg bluegrass	2,610 ± 326^{A}*	2,104 ± 556^{aB}*	1,865 ± 365^{B}*
Woody browse			
Aspen	3,112 ± 560^{bA}	3,005 ± 203^{A}	3,081 ± 252^{A}
Curlleaf mountain mahogany	2,747 ± 332^{A}	2,726 ± 206^{A*}	2,878 ± 202^{A}
Mountain snowberry	3,648 ± 130^{A}	3,185 ± 317^{AB}	2,928 ± 352^{B}
Snowbrush ceanothus	3,057 ± 211^{A}	2,833 ± 113^{A}	2,862 ± 140^{A}
Optimal performance[c]	2,900	2,900	2,750

[a] Outlier removed (*n* = 5).

[b] June 2000 aspen only (*n* = 3).

[c] Optimal performance levels are those that assure animals experience no, or virtually no, limitations from nutrition. Digestible energy optimal performance levels from Cook et al. (In Press).

^{AB}Means in the same row followed by the same uppercase superscript are not different ($P > 0.05$) as tested by Tukey-Kramer HSD tests.

*Estimate less than optimal performance ($P < 0.05$) as tested by 1-tailed, 1-sample *t*-test.

Table 3. Range in mineral concentrations (μg/g) in 12 elk forage species compared to estimated requirements for gestating to early lactating animals and maximum tolerable levels for Ca, K, Mg, Na, P, and S. Reported values are range in mean low and high concentrations across early summer, mid-summer, and early fall, 1999 and 2000 on summer range in the Jarbidge Mountains, Nevada. Requirements and maximum tolerable levels for beef cattle from National Research Council (1996) unless otherwise noted.

	Ca	K	Mg	Na[a]	P	S
	μg/g					
Requirements	1,600–5,800[b]	6,000–7,000	1,000–2,000	600–1,000	1,700–3,900[b]	1,500
Maximum tolerable levels	20,000[b]	30,000	4,000	100,000[bc]	10,000[b]	4,000
Forbs						
Arrowleaf balsamroot	13,000–29,000	12,400–32,333	2,300–2,867	48–62	747–3,467	1,167–3,567
Spurred lupine	13,667–22,333	8,900–21,667	2,400–4,167	36–41	593–2,867	860–2,400
Grasses						
Bluebunch wheatgrass	3,233–8,300	7,100–19,333	1,043–1,233	33–43	420–2,867	983–2,100
Idaho fescue	3,600–8,533	9,433–18,333	887–1,233	24–39	970–2,933	857–1,567
Kentucky bluegrass	3,567–5,500	13,000–22,333	1,007–1,600	39–49	1,233–3,767	1,297–2,500
Mountain brome	3,967–8,733	19,333–40,000	1,367–1,933	32–40	1,030–4,567	1,173–3,833
Needlegrass	4,600–8,967	9,550–18,667	997–1,200	27–41	507–2,367	960–2,233
Sandberg bluegrass	1,867–9,700	4,967–18,667	947–1,567	38–49	633–2,167	823–1,467
Woody browse						
Aspen[d]	9,233–14,267	9,933–18,000	1,867–2,300	N/A[e]	877–2,500	980–1,667
Mountain mahogany	6,867–9,267	4,867–9,533	1,010–1,500	18–52	1,100–2,367	703–1,400
Snowberry	5,967–14,333	12,933–27,333	2,133–3,067	29–29	1,333–3,967	1,100–2,467
Snowbrush ceanothus	8,400–9,933	5,233–12,333	1,150–1,667	18–36	997–3,033	803–1,867

[a] Sodium results from 1999 only. Sodium levels in all 2000 samples were below detectable levels.

[b] National Research Council (1984).

[c] Sodium chloride (table salt).

[d] Aspen not collected in June 1999.

[e] Sodium values for aspen in 1999 were all below detectable levels.

CHAPTER 5

HABITAT USE CONSTRAINTS ON ELK SUMMER NUTRITIONAL CARRYING CAPACITY ESTIMATES

INTRODUCTION

A fundamental objective of wildlife management is to estimate carrying capacity, or the number of animals the resources of an area can support over specific time periods. Carrying capacity proposes that population growth is limited or regulated by abiotic and biotic factors. Carrying capacity for large herbivorous mammals is commonly limited by the availability of forage resources (Reid et al. 1989, Caughley and Gunn 1993). Factors such as snow depth and less easily traversed terrain that limit access to forage resources, or reduced precipitation that decreases forage abundance, may limit ungulate populations through limiting access to, and productivity of forage, respectively (Coughenour and Singer 1996).

In the western United States, >90% of elk (*Cervus elaphus*) summer on public land (Peek et al. 1982) where levels of forage used by livestock are controlled by public land management agencies to provide residual plant matter sufficient to maintain soil, forage plant vigor, livestock diet quality, and wildlife habitat (Holechek 1988). Elk diet selection is largely related to seasonal forage availabilities and comprises a wide range of herbaceous and shrubby species (Cook 2002); however, herbivory pressure from high-density elk populations results in declines in cover and productivity of important structural woody species including aspen (*Populus tremuloides*), big sagebrush (*Artemisia tridentata* spp.), and willows (*Salix* spp.) on summer and winter ranges (Irwin et al. 1994, Singer et al. 1994, Singer and Renkin 1995, Singer et al. 1998, White et al. 1998, Dieni et al. 2000).

Reduced access to forage because of competitive consumption from conspecifics, or from potential competitors like livestock, may regulate population growth and maximum density of wild ungulates such as elk through influencing survival or fecundity rates (Mackie 1978). Excessive grazing by elk on shared rangeland can lead to reductions in adult and calf cattle weight gains (Hobbs et al. 1996). Hobbs et al. (1996) provided experimental evidence that cattle and elk competition occurs when levels of residual herbaceous forage drop below critical thresholds. Competition potential between elk and cattle is a complex issue and depends on range conditions, grazing levels, season of use, and diets. However, cattle and elk temporal grazing patterns rarely overlap on many ranges (Wisdom and Thomas 1996).

Nutritional carrying capacity relates an animal's specific nutritional requirements to the availability of those nutrients in available habitats (McLeod 1997). Estimates of forage quantity through standing crop or biomass, forage quality through nutrient content or digestibility of available food, and nutritional requirements for the specific model animal are needed to estimate nutritional carrying capacity (Robbins 1973, Mautz 1978). Nutritional requirements of wildlife have received extensive attention (see Robbins 1993), but Hobbs and Swift (1985) reported that estimation of nutritional requirements was far ahead of our ability to understand the availability of nutritional resources that meet animal requirements.

An underlying assumption of many habitat evaluation procedures has been that habitat use/availability indices indicate the value of habitats to populations (U.S. Fish and Wildlife Service 1981, Hobbs and Hanley 1990). Hobbs and Hanley (1990) contended that habitat use/availability indices cannot predict carrying capacity unless demographic data support those contentions. Correlations between animal densities and habitat quality can be misleading, with factors including intraspecific interactions, fluctuating resources, and differences in seasonal habitat quality frequently leading to higher densities of animals in poorer quality habitats (Van Horne 1983). Furthermore, Morrison (2001) urged wildlife ecologists to focus on resources when conducting wildlife-habitat relationship studies because resources are the fundamental currencies that allow individuals to survive and reproduce, and habitat use alone generally fails as a predictor of animal performance. Nutritional carrying capacity models considering the influence of habitat use have not been developed. It follows that traditional nutritional carrying capacity estimates have likely been biased towards a higher number of animals than are likely to be supported if those estimates incorporated animal use patterns.

Contemporary nutritional carrying capacity models have focused on ecological carrying capacity (Hobbs and Swift 1985, McCall et al. 1997). Ecological carrying capacity (K_{CC}) is defined as the equilibrium between populations of plants and herbivores in the absence of hunting. By contrast, economic carrying capacity (I_{CC}) is defined as a population equilibrium that allows maximum sustained yield of herbivores without inducing changes in plant community compositions (Caughley 1979, Macnab 1985, Miller and Wentworth 2000). Some recent models have recognized the need to shift away from maximizing numbers of single game species and instead model populations while considering other ecosystem components (deCalesta and Stout 1997, Weisberg et al. 2002). For example, simulation modeling for elk in North Park, Colorado, indicated conservative elk population objectives would avoid promoting negative changes in forage composition such as increases in unpalatable shrubs and herbs and would limit intraspecific competition among elk (Weisberg et al. 2002). Offtake from cervid populations maintained far below K_{CC} is higher due to younger age structures, which consequently provides maximum sustained yield (Miller and Wentworth 2000, McCullough 2001).

Elk provide a workable model to compare nutritional carrying capacity to habitat selection because their habitat and nutritional requirements are relatively well understood (Cook 2002, Skovlin et al. 2002). Lactating female elk provide a particularly compelling model to evaluate relationships between elk summer nutritional carrying capacity and habitat use because their energetic needs in summer are 2 or 3 times higher than during gestation (Robbins 1993), thus their habitat and foraging choices have implications for population productivity (Wisdom and Cook 2000). In addition, pregnancy rates for elk populations may be influenced by availability of nutritious summer-autumn forage (Cook et al. 2001, Cook et al. In press). Cow elk with calves at side must balance summer habitat selection between areas that provide optimal foraging and security conditions to meet demands of neonates and to accumulate sufficient body reserves for future reproduction (Geist 1982).

Our purpose is to develop a nutritional carrying capacity model for elk summer range to estimate population levels that do not alter vegetation conditions. These population levels may be lower than those estimated with I_{CC}; however, economic carrying capacity provides a useful definition of our estimates. For example, minimum-impact carrying capacity occurs at population levels that minimize impacts on other wildlife, vegetation, or humans (Bailey 1984, Miller and Wentworth 2000). Such models are needed by range and wildlife managers to set realistic population objectives on ranges shared by wild and domestic ungulates. In this chapter we use data from an elk population reintroduced into northeastern Nevada to demonstrate how nutritional carrying capacity estimates are constrained by habitat selection.

Specific objectives were to (1) estimate economic nutritional carrying capacity (I_{NCC}) for 236-kg lactating cow elk on summer range at 2 animal performance levels, (2) model cow elk group summer habitat selection with resource selection functions, and (3) adjust I_{NCC} with resource selection functions to reflect habitat selection probabilities. An adjustment to I_{NCC} based on habitat selection probabilities provides a mechanism to constrain populations to levels below those that would promote alteration of key vegetative communities.

Our nutritional carrying capacity model follows these 6 assumptions: (1) I_{CC} models best represent management goals on western rangelands where elk are limited by forage used by or allocated to livestock and other wildlife; (2) at low densities, elk habitat use will be below levels that can appreciably alter resource conditions or plant succession. Higher density elk populations lead to habitat alteration. Elk populations should be managed at levels that maintain biodiversity of plant communities; (3) elk and other ungulates have equal availability to forage resources on the given unit of land evaluated in carrying capacity equations. However, livestock operations may displace elk on portions of summer range (Clegg 1994), thereby reducing access to forage resources; (4) these models are applicable in the absence of large-scale disturbances such as substantial wildfire and/or severe prolonged drought; (5) disease, predation, and competition may limit populations in certain areas, thus reducing carrying capacity; and (6) habitat selection is a dynamic process and changes as population levels change.

STUDY AREA

The study area comprises Nevada Division of Wildlife (NDOW) Hunt Unit 072 (41° 30' to 42° 00' N and 115° 00' to 115° 30' W) in northeastern Nevada (Fig. 1). Hunt Unit 072 consists of 1,665 km^2 with elevations ranging from 1,633 to 3,287 m. We delineated all area ≥2,135 m as elk summer range because 91.3% of cow elk groups relocated on radiotelemetry flights across summers 1998–2001 were found in this region (Fig. 1). Summer range includes 48.2%, or 802 km^2 of the study area, and is administered by Forest Service (91.5%), Bureau of Land Management (5.4%), and private ownership (3.1%). The 392 km^2 U.S. Forest Service Jarbidge Wilderness Area comprises most of the Jarbidge Mountains and 48.9% of the summer range (Fig. 1). Northern slopes drain into the Snake River, while southern slopes drain into the Great Basin (U.S. Forest Service 1981).

Late fall through mid-spring snowpack provides most moisture. Snow water equivalents on 1 April at Natural Resources Conservation Service SNOTEL sites at Pole Creek Ranger Station (2,540 m) in the north and Draw Creek (2,300 m) in the south were 91 and 90%, and 88 and 104% of 1971–2000 averages (Draw Creek, 297 mm; Pole Creek, 523 mm) in 1999 and 2000, respectively. Mean monthly temperatures (ºC) averaged from June through October were 11.3 ± 2.1 in 1999 and 13.6 ± 2.0 in 2000 at Draw Creek, and 9.6 ± 2.4 in 1999 and 11.4 ± 2.0 in 2000 at Pole Creek Ranger Station. June through October cumulative precipitation (mm) was 104 and 41, and 102 and 51, in 1999 and 2000 at Draw Creek and Pole Creek Ranger Station, respectively.

Mountain big sagebrush (*A. t. vaseyana*) and low sagebrush (*A. arbuscula*) interspersed with herbaceous meadows and snowbank associations form a matrix between forested communities. Forested communities include aspen (*Populus tremuloides*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), snowbrush (*Ceanothus velutinus*), and a conifer complex consisting primarily of subalpine fir (*Abies lasiocarpa*), limber pine (*Pinus *flexilis*), and whitebark pine (*P. albicaulis*). Lewis (1975) provided lists of herbaceous species in each community.

Rocky mountain elk (*C. e. nelsoni*) were reintroduced from 1990–95 (Nevada Division of Wildlife 1997) and a population of about 300 (summer range density = 0.4/km^2) were maintained by antlerless harvest from 1996–2000 (Chapter 1). Elk share summer range with mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), cattle, and domestic sheep. Livestock graze 11 sheep, 27 cattle, and 1 common use summer and early fall allotments. Elk calves per 100 cows ratios from 1 July to mid-September 1998–2000 averaged 52 (range = 32–57; Chapter 1), suggesting a productive, growing population with a younger adult female age structure (Wisdom and Cook 2000). Geometric mean finite rates of increase (λ) were 1.08 during the antlerless hunting period (1995–1999) and increased to 1.15 following release from hunting after 1999 (Chapter 1). New population objectives call for elk to increase to 1,000 ± 100 by 2010, when objectives will be reevaluated (Nevada Division of Wildlife 2000).

METHODS

Nutritional Carrying Capacity Model

We estimated economic nutritional carrying capacity (I_{NCC}) for 236-kg cow elk in autumn to reflect expected animal performance under reasonable extreme ranges in digestible energy (DE). Maintenance performance (2,550 kcal/kg) is the DE level required to maintain endogenous energy levels, particularly body fat levels, of adult cows with calves at heel. At maintenance performance, nutritional deficiencies do not yet affect elk performance, but when animals encounter DE levels less than maintenance they will show reduced performance in body condition and reproduction due to limited nutrients (Cook et al. In Press). Optimal performance (2,750 kcal/kg) represented levels where animals would be assured to experience no, or virtually no, limitations from nutrition (Cook et al. In Press). We thus developed the following model to estimate I_{NCC}. We calculated SEs as the square root of the variance for I_{NCC} for each year (i), and 95% CIs as estimated $I_{NCCi} \pm t_{\alpha/2,\, n-1} \times$ SE.

$$\widehat{I_{NCCi}} = \sum_{j=1}^{n}\sum_{m=1}^{5} \frac{\widehat{SDE_{jm}} * \widehat{Use_{jm}} * Area_{jm}}{DMI * DER * Days_i}$$

where

$\widehat{I_{NCCi}}$ = Economic nutritional carrying capacity in autumn of year i,

SDE_{jm} = Mean standing digestible energy (kcal/ha) for forage item j in cover type m,

Use_{jm} = Proportion of forage item j eaten by elk in cover type m,

$Area_{jm}$= Area (ha) of forage item j in cover type m,

DMI = Dry matter intake (kg/day),

DER = Digestible energy required (kcal/kg), and

$Days_i$ = Number of days of autumn in year i.

Variance for the estimator $\widehat{I_{NCCi}}$ was approximated as the variance of a product (Goodman 1960):

$$\widehat{V_{I_{NCCi}}} = \sum_{j=1}^{n}\sum_{m=1}^{5} C_{jm}^{2}\left(\hat{V}\left[(\widehat{SDE}_{jm})(\widehat{Use}_{jm})\right]\right)$$

where

$$C_{jm}^{2} = \left(\frac{Area_{jm}}{(DMI * DER * Day_i)}\right)^{2}$$

and,

$$\hat{V}\left[(\widehat{SDE}_{jm})(\widehat{Use}_{jm})\right] = \left(\widehat{SDE}_{jm}^{2}\right)\left(\hat{V}(\widehat{Use}_{jm})\right)+\left(\widehat{Use}_{jm}^{2}\right)\left(\hat{V}(\widehat{SDE}_{jm})\right)+\left(\hat{V}(\widehat{SDE}_{jm})\right)\left(\hat{V}(\widehat{Use}_{jm})\right)$$

We selected a 236-kg cow elk with calf at side lactating through mid-autumn and with average DMI, activity, and metabolic demands as our model animal (Cook 2002). Elk nutritional requirement calculations have typically considered 236 kg to be an average size for elk cows (Nelson and Leege 1982, Cook 2002). Carrying capacity was estimated for 236-kg lactating cow elk during autumn and based on conditions in 1999 and 2000 in 5 general community types. Autumn, which began on 1 September, was delineated by weather data, with a maximum length of 76 days. Habitat or community type availability, equivalent to the area of cover types, was aspen (121.2 km^2), conifer (85.8 km^2), mahogany (158.3 km^2), sagebrush–herb (414.9 km^2), and snowbrush (21.4 km^2; Appendix 1).

Nutritional parameters incorporated in our carrying capacity model were: (1) DMI for lactating 236-kg cow elk in mid-autumn estimated at 6.9 kg/day (Cook et al. In Press), and (2) DE content (kcal/kg) required to provide maintenance performance (2,550) and optimal performance (2,750) for lactating 236-kg cow elk in early fall (Cook et al. In Press); the product of these parameters yields an average requirement of 17,595 and 18,975 kcal/day, respectively. Standing digestible energy (SDE; kcal/ha), the currency of our model was approximated as the product of DE (kcal/kg) and standing crop (kg/ha). Early fall SDE in key forages was estimated in aspen, conifer, mahogany, sagebrush–herb, and snowbrush communities. Standing crop estimates represented residual forage available, following livestock grazing. Key forages were identified in elk feeding sites and through microhistological fecal analysis (Chapter 2, Appendix 2).

Proportions of forage items eaten by elk represent mean use of perennial forbs, perennial graminoids, and woody browse observed at elk feeding sites (Appendix 2). Estimated elk use in forested communities was 10.1 ± 2.9% (± SE), 4.5 ± 2.2%, and 0.9 ±

0.3% for perennial forbs, woody browse, and perennial graminoids, respectively. In sagebrush–herb communities, estimates were 9.1 ± 1.8%, 3.5 ± 1.7%, and 1.3 ± 0.3% for perennial forbs, woody browse, and perennial graminoids, respectively. We used Hobbs and Swift's (1985) nutritional carrying capacity algorithm to adjust estimated proportion of forage used in mixed diets for elk selecting maintenance and optimal performance diets (Cook et al. In Press). We accordingly proportionally adjusted the variance of each proportionally adjusted carrying capacity estimate. These adjustments constrained our model downward by removing low quality forage (Hobbs and Swift 1985). Perennial graminoids in aspen, conifer, and sagebrush–herb communities in 1999 and 2000 and in mahogany in 2000 were removed from I_{NCC} estimates after the algorithm indicated DE content was too low to provide a mixed diet meeting cow elk requirements for maintenance performance in autumn. Perennial graminoids were likewise removed from autumn 1999 and 2000 I_{NCC} estimates in aspen, conifer, mahogany, and sagebrush–herb communities because they did not provide energy sufficient to meet cow elk requirements for optimal performance. Appendix 2 contains detailed sections outlining each portion of our nutritional carrying capacity model.

Elk Group Habitat Selection

Ten cow elk were captured on winter ranges in 1998 and 7 cows in 2000 with netguns shot from helicopters to facilitate attachment of VHF radio collars (Telemetry-Electronics Consultants, Inc., Mesa, Arizona, USA). One cow collared in 1998 summered outside of the study area. Radio-collared cows provided locations of elk groups composed primarily of cows, calves, and yearling bulls. Cessna 206 Turbo fixed wing aircraft were used to systematically sample locations of all cow elk groups by searching for each collared elk during morning hours 1–4 weeks apart during summers 1998–2000. The 2 flights conducted in 2001 were 8 weeks apart. A NDOW biologist recorded group locations through ocular observations or by strength of signal of collared elk. The dominant cover type in which each elk group was located was also recorded. Locations were recorded in the air on a 1:100,000 topographic map, and in 2000, some locations were recorded with a hand-held global positioning system unit. We later plotted locations in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA, 1992–2002) to derive Universal Transverse Mercator (UTM) coordinates.

We located radio-collared cow elk groups on the ground following summer relocation flights to provide a count of the number of cows and yearling bulls in each group. We averaged low and high group sizes in those instances where collared cows were located more than once following flights. We multiplied mean cow group sizes for each collared cow (including collared cows) from ground counts following each flight by the number of collars located on each flight. We divided these products by the estimated population of adult cows and yearling bulls and then multiplied by 100 to indicate the percentage of the adult cow and yearling bull population located on each flight. Nevada Division of Wildlife minimum population estimates for adult cows and yearling bulls were 202 (0.6227 of total *N*) in 1998; 198 (0.6139 of total *N*) in 1999; and 185 (0.6823 of total *N*) in 2000 (J. Williams, NDOW, personal communication 2003).

We defined 1 June through mid-September, prior to opening dates of antlerless elk rifle hunts, to be the summer period. Elk group locations from flights prior to 1 June tended to be at lower elevations than those after 1 June and those after mid-September tended to be in more remote areas with more forested habitats than those in summer. We considered flights, not individual elk groups to be observational units with groups located during each flight being samples within flights.

Our sampling approach followed Design 2 of Thomas and Taylor (1990) and Erickson et al. (2001), where use was identified for each individual group, and availability was defined for the population at each flight. Noncontiguous buffers with 2.3 km radii were placed around each elk group and random location. Buffer radii represented the median distance collared cow elk moved between relocation flights. Distances of individual cows were evaluated because group membership frequently changed. The distribution of movements was skewed right, indicating the need for use of nonparametric methods; thus the median distance moved represented the area most likely used (50%) by elk groups between successive locations. The area bounded by buffers with radius equal to the 2.3 km median (1,677.8 ha) were analogous to 50% elk group home ranges, thus providing an analysis corresponding to Johnson's (1980) second order of selection. Evaluation of habitat components within buffers provided an analysis equivalent to Johnson's (1980) third selection order.

Habitat variables at each elk group location were weighted by number of radio-collared elk in each group. Elk data were summarized by 19 relocation flights (1998 = 3; 1999 = 7; 2000 = 7; 2001 = 2). Random locations were also averaged according to 19 random groupings of noncontiguous buffers equal to the number of elk groups located during each flight. During each flight, use was identified for each elk group within noncontiguous buffers, while availability was evaluated in paired buffers of equal size placed at a random azimuth and within 4.6 km of the center of each elk group buffer. Paired, non-overlapping buffers facilitated evaluating habitat selection as a conditional fixed-effects model, where habitat at elk locations was compared to habitat at random locations representing habitat availability (Lancaster and Imbens 1996). We took the conservative approach of clipping buffers within the extent of the summer range to set all habitat evaluations on an equivalent scale. Buffers overcame error and bias in locations while evaluating the mosaic of habitats encountered in the study area (Rettie and McLoughlin 1999).

A principal assumption of habitat use-availability studies is that availability remains constant over the period of study (Alldredge et al. 1998, Erickson et al. 2001). A 121.4-km^2 fire on the eastern slope of the Jarbidge Mountains occurred in early August 2000. Most of the burned area was below 2,135 m and in sagebrush. This fire did not change overall summer habitat composition, and the distribution of summer telemetry locations after this date did not change from previous summer locations.

Geographic Data

We obtained data for our habitat selection model from geographic data coverages. Our roads coverage was obtained from a U.S. Census Bureau 2000 Tiger® digital line graph file at 1:100,000 scale. All roads were gravel and unimproved and were evaluated as one road category. The perennial streams coverage was developed from USGS 1:100,000 scale digital line graph data (1997 U.S. Bureau of Land Management, Nevada State Office, Mapping Sciences, Nevada Perennial Streams, Reno, Nevada, USA). Distance to perennial streams were considered in part because Nevada Division of Wildlife (1997) considered free water to potentially be the only real limiting factor to elk population growth in the state. Distances (m) from elk group and random buffer centers to nearest road and perennial stream arcs were evaluated with the near command in ArcGIS 8.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA, 1992–2002).

Raster data were spatially analyzed in ArcGIS 8.3 GRID module. We used a 30 m USGS digital elevation model to compute elevation (m), slope (%), and aspect. Mean elevation and percent slope were tabulated in each 2.3-km buffer. Slope proportions were arcsine square root transformed to meet assumptions of normality and equal variance. Aspect was reclassified as flat (no aspect), cool (N, E, NE, NW), or warm (S, W, SW, SE). We evaluated percentage of cool aspect in each buffer because elk often select north-facing topographical relief during summers (Julander and Jeffrey 1964, Skovlin et al. 2002).

We used ERDAS IMAGINE 8.5 (ERDAS®, Inc., Atlanta, Georgia, USA) to create a cover type availability map (map accuracy = 89.6%) representing composition of aspen, conifer, mahogany, sagebrush–herb, and snowbrush on the summer range (Appendix 1). Our cover type map was created with three Landsat 7 Enhanced Thematic Mapper (ETM+) scenes with ground resolution of 30 m (Homer et al. 2002; map projection, UTM Zone 11; datum, NAD 1927) by: (1) conducting a principal components analysis with the original data to reduce the data dimensionality from 6 bands to 3, (2) performing an unsupervised classification on the principal components image, and (3) masking and merging the 3 classified images to produce one continuous map without cloud and shadow (Appendix 1). We tabulated areas of cover in each buffer to compute cover percentages in each buffer.

Cover types in buffers around location points formed a composition, or proportion of all covers in each buffer summed to 1 (i.e., the unit sum constraint; Alldredge et al. 1998). We transformed cover type proportions with the arcsine square root transformation to meet assumptions of normality and equal variance when cover types were considered separately in

1 variable models. We compensated for the unit sum constraint in 2 variable models by computing natural log ratios of cover types (Aebischer et al. 1993) with the focal sum function in ArcGIS 8.3. Natural log ratios were computed to avoid comparing linear combinations of vegetation cover and these ratios normalized and equalized variances for cover data. Natural log ratios were aspen/snowbrush (X1), aspen/conifer (X2), mahogany/snowbrush (X3), and sagebrush/snowbrush (X4). Aspen was incorporated in 2 natural log ratios to evaluate the relative value of aspen to other cover types because aspen is known for its abundant, high quality forage (DeByle 1985).

Habitat Selection Modeling

Variables included in habitat modeling were distances (m) to the nearest perennial stream (H2O) and road (ROAD), mean elevation (ELEV), mean percent slope (SLOPE), percentage of cool aspect in each buffer (COOL), the arcsine square root of proportions of aspen (ASPEN), conifer (CONIFER), mahogany (MAHOG), sagebrush–herb (SAGE), and snowbrush (SNOW) in each buffer, and X1, X2, X3, and X4 natural log ratios of vegetation covers. We used paired *t*-tests to evaluate differences in habitat variables between elk group locations and available habitat represented through random locations (PROC TTEST; SAS Institute 2001). We assessed multicollinearity between variables with a Pearson's correlation matrix and removed 1 variable from each correlated pair when $r \geq 0.60$ (Proc CORR; SAS Institute 2001). We used a multivariate analysis of variance (MANOVA; Proc GLM; SAS Institute 2001) with YEAR as a single main effect to evaluate differences between yearly elk group habitat selection to pool data across the 4 years of our study (Schooley 1994).

We used binary logistic regression to evaluate summer cow elk group habitat selection with elk group locations compared to paired random locations (Proc LOGISTIC; SAS Institute 2001). Our logistic regression model provided a fit to independent habitat variables where the dependent data were 1 for used units and 0 for available units (Boyce and McDonald 1999). Logistic regression modeling examined 6 major hypotheses explaining elk habitat selection in our study area: (1) forage, (2) forage and roads, (3) forage and topography, (4) forage and water, (5) roads and water, and (6) topography and distances to landscape features. We evaluated model fit in 2 and 3 parameter models (intercept denoted as 1 parameter) to avoid overfitting models with too many parameters.

We assessed the strength of evidence for each model with Akaike's information criterion bias-correction for small samples (AIC_c), where K = number of parameters, and n = sample size (Burnham and Anderson 1998):

$$AIC_c = AIC + 2K(K + 1) / n - K - 1 \qquad (1)$$

The model with the lowest AIC_c value was selected as the best model, and ΔAIC_c the difference between AIC_c for the best model and AIC_c for all other candidate models was used to identify models competing with the best model. Models with $\Delta AIC_c \leq 2$ were competitive with the best model, and models with $\Delta AIC_c \geq 4$ were poor fitting models (Burnham and Anderson 1998).

We used the best logistic regression model to estimate resource selection function (w[**x**]) coefficients based on a vector **x** of independent habitat variables. In this model, exp is the natural exponent. Resource selection functions are probabilities proportional to use of resource units (Manly et al. 2002).

$$\mathrm{w}(\mathbf{x}) = \exp(\beta_o + \beta_1 x_1 + \beta_2 x_2) \tag{2}$$

Relative use, $U(\mathbf{x}_i)$, of each pixel on our habitat availability map was calculated as follows, where $A(\mathbf{x}_i)$, the area of each habitat pixel = 900 m^2 (0.09 ha; Boyce and McDonald 1999):

$$U(\mathbf{x}_i) = \mathrm{w}(\mathbf{x}_i)\, A(\mathbf{x}_i) \,/ \sum \mathrm{w}(\mathbf{x}_j) A(\mathbf{x}_j) \tag{3}$$

Density, $D(\mathbf{x}_i)$, of 236-kg cow elk under maintenance and optimal performance levels in each cover type were obtained by multiplying I_{NCC} estimated for each year (i) and performance level by relative use adjusted by area for each cover type (Boyce and McDonald 1999):

$$D(\mathbf{x}_i) = I_{NCCi} * U(\mathbf{x}_i) \,/\, A(\mathbf{x}_i) \tag{4}$$

We examined differences between yearly I_{NCC} estimates at both performance levels redistributed as RSF densities (RSFD) in each cover type as I_{NCC} – RSFD, when RSFD densities exceeded original I_{NCC} estimates. We adjusted our estimates in this manner to avoid estimates that would promote overuse of forage in communities. These adjustments also avoid the problem of setting population objectives based on estimates that cannot support the number of animals the forage in those communities can sustain in autumn.

Cross Validation Procedure

We applied the logistic regression probability function to our 30 m resolution habitat availability map according to the best model identified through AIC$_c$ to derive a spatially explicit habitat selection probability grid for 2.3-km buffer sizes.

$$\tau(\mathbf{x}) = \exp(\beta_o + \beta_1 x_1 + \beta_2 x_2) / (1 + \exp[\beta o + \beta_1 x_1 + \beta_2 x_2]) \quad (5)$$

We used the moving window operation in ArcGIS 8.3 GRID to create this spatially explicit grid. Moving window operations consider pixels in raster data sets on a case-by-case basis. We used the conditional function in ArcGIS 8.3 GRID to substitute 1 in cover type ratio calculations when the value of aspen or conifer was 0 within a moving window to avoid computational problems inherent when dividing with zeroes. The moving window operation considered 18,627 pixels (77 x 30 m = 2,310 m radius) at the 2.3-km scale. All grid calculations associated with resource selection functions were computed within these moving window regions.

We performed a 5-fold cross validation to evaluate goodness-of-fit of our habitat selection model (Boyce et al. 2002). We divided elk group and random observations randomly into 5 cross validation groups. Cross-validation iterative procedures modeled 4 of the 5 data sets using logistic regression (PROC LOGISTIC; SAS Institute 2001; Boyce et al. 2002). We estimated parameters in the reduced best model identified with AIC$_c$. We evaluated model performance by examining predicted probabilities of elk presence for validation testing data against the actual elk presence, with the predicted probabilities grouped into bins. Predicted probabilities were sorted and placed into 10 groups with the first 9 containing 4 values and the last containing 2 values. Bins were ranked according to increasing probabilities of elk presence. Within each of the 10 groups, the ratio of observations with observed elk occurrence was calculated. A Spearman's rank correlation (PROC CORR; SAS Institute 2001) was calculated between bin ranks and cross-validated predictions of elk presence. A strong positive correlation would indicate our model had good predictive performance, because more elk locations would fall into higher ranked probability bins (Boyce et al. 2002).

RESULTS

Nutritional Carrying Capacity

We approximated autumn 1999 to be 53 days and autumn 2000 to be 76 days in length. Maintenance performance I_{NCC} estimates for 236-kg lactating cow elk were 2,533 (95% CI: 1,277–3,789) in 1999 and 1,655 (95% CI: 856–2,454) in 2000. Optimal performance I_{NCC} estimates for 236-kg lactating cow elk were 2,264 (95% CI: 1,104–3,424) in 1999 and 1,100 (95% CI: 348–1,852) in 2000. Summer range densities calculated with I_{NCC} estimates based on maintenance performance were 3.2/km^2 in 1999 and 2.1/km^2 in 2000 and densities calculated with I_{NCC} estimates based on optimal performance were 2.8/km^2 in 1999 and 1.4/km^2 in 2000.

Elk Group Habitat Selection

Elk use the summer range for at least 7 months of each year. We base this on the fact that 197/232 (84.9%) of radiomarked cow elk relocations from 25 April to 23 October 1998–2001 were found in this region, and elk used portions of the summer range throughout each year, selecting different topography and communities according to weather conditions (J. Williams, NDOW, personal communication, 1998). We obtained 175 locations from 16 radio-marked elk cows (mean locations per cow = 10.1 [range = 1–19]) on 19 flights across summers 1998–2001. Of these locations, 162 of 175 (92.6%) occurred on summer range. Individual elk cows (8.5 ± 0.7 [± SE] individual elk located/flight) provided locations of 136 independent elk groups (7.2 ± 0.8 elk groups/flight) on summer range (Table 1). Cow elk groups located with radio-collared cows represented 5.9–111.4% of combined adult cow and yearling bull estimates (Table 1). Groups located in early June were smallest (5.9–10.1%), reflecting the period when cows separate to calve or tend to neonates. However, by mid-to late August, cow elk nursery groups located with radio-marked elk cows represented 95.5–111.4% of estimated adult cows and yearling bulls in the population (Table 1).

Removing correlated variables reduced the set of habitat variables to ROADS, H2O, COOL, MAHOG, X2 and X4. Results from MANOVA provided justification to pool elk group habitat selection data at the 2.3-km buffer scale across summers 1998–2001 (Wilk's $\Lambda = 0.19$, $F_{18,28} = 1.29$, $P = 0.263$). Elk groups used habitats closer to perennial streams (511.5 ± 62.7 m) and roads (1,920 ± 221.4 m) than at random (perennial streams, 878.7 ± 94.2 m; roads, 2,516.2 ± 236.7 m; Table 2). Elk groups selected habitats with lower slopes than at random (elk, 32.6 ± 0.5%; random, 36.0 ± 0.7%). Percentage cover type in 2.3-km elk buffers was comprised of higher ($P < 0.001$) aspen and snowbrush and less ($P < 0.001$) conifer than available as evaluated in random 2.3-km buffers (Table 2). There was no difference between elk-used and random locations for cool aspect, elevation, mahogany cover, or sagebrush–herb cover (Table 2).

The best model, which included X2 and H2O ($AIC_c = 18.290$), provided evidence in support of water and forage influencing habitat selection. No other models were competitive candidate models ($\Delta AIC_c \geq 14.252$) with the best model (Table 3). The best model variables (X2 and/or H2O) were included in the first 7 candidate models. Further, a separate analysis using logistic regression best subsets modeling with the score criterion indicated the combination of X2 and H2O model was the most parsimonious model that best fit the data. The parameter estimate for H20 (-0.0144 ± 0.0073, $P = 0.047$) suggests the probability of elk groups selecting habitat decreased slightly as the distance to water increased. The parameter estimate for X2 (14.5782 ± 8.0748, $P = 0.071$) indicates the probability of elk groups selecting areas greatly increased as the amount of aspen cover increased relative to conifer cover (Fig. 2).

Cross validation results indicated our model was a strong, positive predictor of elk habitat selection ($r_s = 0.86$, $P = 0.002$, $n = 10$). The model was particularly good at predicting elk habitat selection from random locations (Fig. 3). A map spatially depicting probabilities of elk group habitat use indicates: (1) highest probability of use ($P \geq 0.95$) in the Canyon Creek and Elk Mountain areas in the northeast and the southern portion of the Jarbidge Wilderness and (2) lowest probability of use ($P \leq 0.10$) in the central and northern portions of the Jarbidge Wilderness (Fig. 4). Distribution of each cover type among probability of use classes was bimodal (Fig. 5). Conifer had the highest proportion of area (0.69) within the lowest probability class ($P \leq 0.10$), followed by mahogany (0.48), aspen and sagebrush–herb (0.34), and then snowbrush (0.29). Snowbrush had the highest proportion of area (0.59) in the highest probability of use class ($P \geq 0.95$), followed by sagebrush–herb (0.56), aspen (0.54), mahogany (0.40), and conifer (0.18; Fig. 5).

Nutritional Carrying Capacity Adjusted with Resource Selection Functions

Maintenance performance I_{NCC} estimates adjusted with RSFDs resulted in 751 fewer elk in 1999 (adjusted I_{NCC} = 1,782; density = 2.2/km^2) and 456 fewer elk in 2000 (adjusted I_{NCC} = 1,199; density = 1.5/km^2), corresponding to 29.6% and 27.6% decreases in original 1999 and 2000 maintenance performance I_{NCC} estimates, respectively (Table 4). Maintenance performance I_{NCC} differences in 1999 were attributed to an increase of 90 cow elk in aspen communities and 661 cow elk in sagebrush–herb communities above I_{NCC} estimates as predicted with RSFDs. The difference between 2000 I_{NCC} maintenance performance estimates and RSFDs was a prediction of 17 cows in aspen communities and 439 cows in sagebrush–herb communities above I_{NCC} estimates (Table 4).

Optimal performance I_{NCC} estimates adjusted with RSFDs resulted in 637 fewer elk in 1999 (adjusted I_{NCC} = 1,627; density = 2.0/km^2) and 478 fewer elk in 2000 (adjusted I_{NCC} = 622; density = 0.8/km^2). Adjusted estimates corresponded to 28.1% and 43.5% decreases in original 1999 and 2000 optimal performance I_{NCC} estimates, respectively (Table 4). Optimal performance I_{NCC} differences in 1999 were attributed to an increase of 83 cow elk in aspen and 554 cow elk in sagebrush–herb communities greater than I_{NCC} estimates as predicted with RSFDs. The difference between 2000 I_{NCC} optimal performance estimates and predicted RSFDs was 6 cows in aspen and 472 cows in sagebrush–herb communities above I_{NCC} estimates (Table 4). Each year, RSFDs predicted fewer elk would use conifer, mahogany, and snowbrush communities than the original I_{NCC} model predicted.

DISCUSSION

Carrying capacity estimates in 2000 represented average snowpack water year conditions followed by a warmer summer with less than 50% of the precipitation as in 1999, another normal snowpack year. Length of autumn 2000 was maximum at 76 days; thus estimates using 2000 data provide a reasonable approximation of carrying capacity for long, dry autumns when forage production and/or nutrients are limited. Both 1999 and 2000 estimates reflect average snowpack conditions, but the 2000 estimates are more realistic because these estimates characterize foraging conditions in a dry and hot summer. Winter range forage resources may limit or regulate elk population growth at levels below what forage availability on summer range will. Summer range nutritional carrying capacity estimates adjusted with RSFDs may thus be generous considering that (1) elk likely use portions of summer range in fall for periods longer than the approximated lengths of autumn and that (2) winter range forage resources may be more limiting to elk in the area than summer range forage resources. Alteration of favored areas is likely to occur as elk reach densities approaching I_{NCC} estimates.

Our results suggest increases in aspen cover and free water and decreases in conifer cover and livestock use of forage would all contribute to increased I_{NCC} for elk in the Jarbidge Mountains. In particular, the abundance and productivity of aspen communities is paramount to the future productivity of this elk population. Highest probabilities of elk use were predicted to be in areas where aspen was in higher abundance than conifer. Aspen habitats across the West are known for their lush undergrowth of shrubs, grasses, and in particular forbs (Mueggler 1988). Elk may select aspen over other forest types and openings in summer due to abundant, high quality forage (DeByle 1985). Delayed phenological development under cool, moist cover prolongs forage quality in aspen understories. In northern Nevada, 80% of aspen stands occur at 1,981–2,347 m elevation (modal elevation = 2,070 m), typically in moist sites or where snow accumulates (Mueggler 1988). Snowbrush grows adjacent to or in aspen in snowbank associations throughout the study area. Furthermore, spectral reflectance for snowbrush and aspen is similar. Thus, the high level of elk selection we detected for snowbrush, although it only comprised 2.6% of the area above 2,135 m, was likely related to association with aspen (Rettie and McLoughlin 1999).

Redistributing carrying capacity estimates with resource selection functions provided a useful tool to predict distributions of animals estimated under different performance levels and under differing yearly foraging conditions. Managers setting population objectives based on traditional carrying capacity estimates not constrained by probabilities of habitat use likely have contributed to population levels that have altered vegetation in key foraging areas. Coupling resource selection functions with animal densities has heretofore focused on estimating population size and distribution in new areas with densities from similar habitats in other areas (Boyce and McDonald 1999, Manly et al. 2002, Boyce and Waller 2003). Our analysis demonstrates how resource selection functions can be used to adjust carrying capacity estimates. These procedures could be extended to estimate and subsequently adjust carrying capacities for new populations when information on nutrient and habitat availabilities, and probabilities of habitat selection for the selected species are available from similar areas.

MANAGEMENT IMPLICATIONS

The 2000 maintenance performance estimate adjusted with RSFDs (1,199; summer range density = 1.5/km^2) should serve as a benchmark for the Jarbidge population to avoid alteration of forage resources. This density is similar to 1.4 elk/km^2 estimated for the adjacent 872-km^2 Bruneau River watershed (U.S. Forest Service 1994). This population objective will ensure provision of ample nutritious resources during lean periods to an elk population level that should not appreciably alter vegetation conditions. Adjustments to carrying capacity estimates with resource selection functions provide a mechanism to avoid overuse of key foraging communities. Monitoring aspen and sagebrush–herb communities in the Jarbidge Mountains is especially important to ensure overuse does not occur as populations expand.

The need to maintain population objectives in line with forage resources is further born out by the fact that Nevada Division of Wildlife (1997) reported a statewide average ratio of 42 calves per 100 cows, lower than reported in adjoining states. Although these ratios may be affected by a later winter census period than in adjoining states (Nevada Division of Wildlife 1997), quantity and quality of forage resources to a large degree translates to ungulate population performance. An observed ratio of 32 calves per 100 cows in 2000 in the Jarbidge Mountains represented a decline of 43.9 and 39.6% from ratios in 1998 and 1999, respectively (Chapter 1). Lower calf numbers probably reflected drier and warmer conditions across summer 2000 that adversely affected foraging conditions and led to lower calf survival. Herbage yields in Great Basin sagebrush communities can realistically vary by at least 2-fold between dry and wet years (Ganskopp and Bohnert 2001). Prudent management should consider the effects of reduced foraging conditions on elk populations during dry autumn periods.

Carrying capacity estimates based on lactating cow elk should not be adjusted to reflect elk population composition. A conservative approach would be to only base elk population objectives on the number of lactating cows supportable in dry years, thus providing ample nutritious resources to the entire population regardless of sex or age as forage resources wane during lean years. Further caution is expressed when estimating elk carrying capacity for aspen habitats as browsing pressure from high-density elk populations severely limits aspen regeneration (White et al. 1998, Dieni et al. 2000). This is especially imperative, as aspen habitats across the Intermountain West have declined 60% from historical levels (Bartos 2001).

Roads have been identified as the primary factor affecting habitat effectiveness for elk (Lyon 1983, Rowland et al. 2000, Skovlin et al. 2002). Although elk in our study selected habitats that were closer to roads than at random, they still were nearly 2 km on average from roads. Roads were placed in areas of low to moderate relief due to the rugged nature of the terrain in the study area. In addition, roads were commonly placed in aspen and sagebrush–herb cover types, which dominate the summer range outside the wilderness area. The remoteness of the study area likely contributed to a reduced effect of roads on elk habitat selection; however, road densities are clearly higher in many areas selected by elk. Future management should consider the effects of road construction and traffic frequency in areas of high probability use. Increased traffic and/or road densities will reduce the effectiveness of habitat for elk in the Jarbidge Mountains.

Elk populations have typically been managed at high densities in the western United States and density dependent processes clearly occur in populations as they reach carrying capacity (Singer et al. 1998, Wisdom and Cook 2000). It is not known if the Jarbidge elk population will exhibit density dependent responses such as lower calf survival, declining population growth, and reduced antler and body sizes as they reach our adjusted I_{NCC} estimates. However, as ungulate densities increase, favored forage species decline, which can lead to animals selecting less preferred forage of lower nutritional quality (Kie et al. 1980, Irwin et al. 1994). Reduced nutritional conditions can then adversely affect population health, condition, and population parameters (Kie et al. 1980, Irwin et al. 1994). Maximum sustained yield theory suggests populations are most productive when they are maintained at species-specific levels far below K_{CC} (McCullough 2001, Wisdom and Cook 2000). It is clear that maintaining this elk population at or below the adjusted I_{NCC} levels we have estimated will assist in maintaining population productivity while not overly jeopardizing the vegetation resources that sustain these elk and other ungulates in this arid region.

LITERATURE CITED

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Alldredge, J. R., D. L. Thomas, and L. L. McDonald. 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:237–253.

Bailey, J.A. 1984. Principles of wildlife management. John Wiley & Sons, New York, New York, USA.

Bartos, D.L. 2001. Landscape dynamics of aspen and conifer forests. Pages 5–14 *in* W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, compilers. Sustaining aspen in western landscapes: symposium proceedings. U.S. Forest Service, Proceedings RMRS-P-18, Fort Collins, Colorado.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

_____, P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–300.

_____, and J. S. Waller. 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. Wildlife Society Bulletin 31:670–683.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information–theoretic approach. Springer-Verlag, New York, New York, USA.

Caughley, G. 1979. What is this thing called carrying capacity? Pages 2–8 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming, Laramie, USA.

_____, and A. Gunn. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. Oikos 67:47-55.

Clegg, K. 1994. Density and feeding habits of elk and deer in relation to livestock disturbance. Thesis, Utah State University, Logan, Utah, USA.

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

_____, B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. In Press. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs.

Cook, R. C., D. L. Murray, J. G. Cook, P. Zager, and S. L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology 79:845–853.

Coughenour, M. B., and F. J. Singer. 1996. Elk population regulation processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573–593.

DeByle, N. V. 1985. Wildlife. Pages 135–152 *in* N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. U.S. Forest Service, General Technical Report RM-119, Fort Collins, Colorado.

DeCalesta, D. S., and S. L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildlife Society Bulletin 25:252–258.

Dieni, J. S., B. L. Smith, R. L. Rogers, and S. H. Anderson. 2000. Effects of ungulate browsing on aspen regeneration in northwestern Wyoming. Intermountain Journal of Sciences 6:49–55.

Erickson, W. P., T. L. McDonald, K. C. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pages 209–242 *in* J. J. Millspaugh, and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Ganskopp, D., and D. Bohnert. 2001. Nutritional dynamics of 7 northern Great Basin grasses. Journal of Range Management 54:640–647.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219–277 *in* J.W. Thomas and D.E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Goodman, L. A. 1960. On the exact variance of products. Journal of the American Statistical Association 55:708–713.

Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management 54:515–522.

_____, and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.

_____, D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. Ecological Applications 6:218–227.

Holechek, J. L. 1988. An approach for setting the stocking rate. Rangelands 10:10–14.

Homer, C., C. Huang, L. Yang, and B. Wylie. 2002. Development of a circa 2000 land cover database for the United States. In 2002 American Society for Photogrammetry and Remote Sensing–American Congress on Surveying and Mapping Annual Conference and FIG XXII Congress Proceedings, April 19–26, Washington, D.C.

Irwin, L. L., J. G. Cook, R. A. Riggs, and J. M. Skovlin. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystems. U.S. Forest Service General Technical Report PNW-GTR-325.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Julander, O., and D. E. Jeffrey. 1964. Deer, elk and cattle range relations on summer range in Utah. Transactions of the North American Wildlife and Natural Resources Conference 29:404–413.

Kie, J. G., D. L. Drawe, and G. Scott. 1980. Changes in diet and nutrition with increased herd size in Texas white-tailed deer. Journal of Range Management 33:28–34.

Lancaster, T., and G. Imbens. 1996. Case-control studies with contaminated controls. Journal of Econometrics 71:145–160.

Lewis, M. E. 1975. Plant communities of the Jarbidge Mountain complex, Humboldt National Forest. Report to Intermountain Region, U.S. Forest Service, Ogden, Utah.

Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. Journal of Forestry 81:592–595.

Mackie, R. J. 1978. Impacts of livestock grazing on wild ungulates. Transactions of the North American Wildlife Conference 43:462–476.

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. Wildlife Society Bulletin 13:403–410.

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

Mautz, W. W. 1978. Nutrition and carrying capacity. Pages 321–348 *in* J. L. Schmidt and D. L. Gilbert, editors. Big game of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

McCall, T. C., R. D. Brown, and L. C. Bender. 1997. Comparison of techniques for determining the nutritional carrying capacity for white-tailed deer. Journal of Range Management 50:33–38.

McCullough, D. R. 2001. Population manipulations of North American deer *Odocoileus* spp.: balancing high yield with sustainability. Wildlife Biology 7:161–170.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environments? Oikos 79:529–542.

Miller, K. V., and J. M. Wentworth. 2000. Carrying capacity. Pages 140–155 *in* S. Demarias and P.R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613–623.

Mueggler, W.F. 1988. Aspen community types in the Intermountain Region. U.S. Forest Service, General Technical Report, INT-250, Ogden, Utah.

Nelson, J. R., and T. A. Leege. 1982. Nutritional requirements and food habits. Pages 323–367 *in* J. W. Thomas and D.E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania.

Nevada Division of Wildlife. 1997. Nevada elk species management plan. Nevada Division of Wildlife, Reno, Nevada, USA.

_____. 2000. Sub-plan for elk management in the Jarbidge Mountains, Nevada. Nevada Division of Wildlife, Reno, Nevada, USA.

Peek, J. M., R. J. Pedersen, and J. W. Thomas. 1982. The future of elk and elk hunting. Pages 599–625 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America, ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Reid, D. G., H. Jinchu, D. Sai, W. Wei, and H. Yan. 1989. Giant panda *Ailuropoda melanoleuca* behaviour and carrying capacity following a bamboo die-off. Biological Conservation 49:85–104.

Rettie, W. J., and P. D. McLoughlin. 1999. Overcoming radiotelemetry bias in habitat-selection studies. Canadian Journal of Zoology 77:1175–1184.

Robbins, C. T. 1973. The biological basis for the determination of carrying capacity. Dissertation, Cornell University, Ithaca, New York, USA.

_____. 1993. Wildlife feeding and nutrition, second edition. Academic Press, San Diego, California, USA.

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.

SAS Institute. 2001. SAS/STAT User's Guide, Release 8.2. SAS Institute, Incorporated, Cary, North Carolina, USA.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management 58:367–374.

Singer, F. J., L. C. Mack, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

_____, and R. A. Renkin. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Naturalist 55:201–212.

_____, D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968–1993. Wildlife Society Bulletin 26:375–390.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Habitat selection and evaluation. Pages 531– 555 *in* J. W. Thomas and D. E. Toweill, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C.

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.

U.S. Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models. Ecological services manual 103. U.S. Fish and Wildlife Service, Washington, D.C.

U.S. Forest Service. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. U.S. Forest Service, Humboldt National Forest, Elko, Nevada.

_____. 1994. Decision notice and finding of no significant impact for the Bruneau River watershed environmental assessment. U.S. Forest Service, Humboldt National Forest, Elko County, Nevada.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Weisberg, P. J., N. T. Hobbs, J. E. Ellis, and M. B. Coughenour. 2002. An ecosystem approach to population management of ungulates. Journal of Environmental Management 65:181–197.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin 26:449–462.

Wisdom, M. J., and J. G. Cook. 2000. North American elk. Pages 694–735 in S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

_____, and J. W. Thomas. 1996. Elk. Pages 157–181 in P. R. Krausman, editor. Rangeland wildlife. The Society for Range Management, Denver, Colorado, USA.

Table 1. Cow elk group population representation following telemetry flights to relocate collared cows, Jarbidge Mountains, Nevada, summers 1998–2001. Sixteen radio-marked cows (9 in 1998; 7 in 1999; and 12 in 2000) were used to locate elk groups on summer range. Ground counts following flights in 1998–2000 provided a measure of the number of adult cows and yearling bulls with each collared cow. Mean number of adult cows and yearling bulls with each cow (including that collared cow) located on ground following each flight were multiplied by number of collars/flight and compared to total adult cow and yearling bull estimates to indicate population representation for each flight.

Flight	Aerial relocations		Ground counts			Representation[a]	
	Groups	Collars	*n*	Mean	SE	Total	%[b]
1998							
8 Jun	2	2	2	7.8	1.8	16	7.9
28 Jul	4	8	9	16.7	2.6	134	66.3
28 Aug	3	8	8	28.1	2.1	225	111.4
1999							
9 Jun	5	5	1	4.0	0.0	20	10.1
16 Jun	7	7	N/A	N/A	N/A	N/A	N/A
30 Jun	4	5	1	17.5	0.0	88	44.4
7 Jul	5	6	5	27.0	8.0	162	81.8
14 Jul	4	6	1	19.5	0.0	117	59.1
11 Aug	5	7	1	27.0	0.0	189	95.5
1 Sep	4	6	1	7.0	0.0	42	21.2
2000							
1 Jun	10	11	1	1	0.0	11	5.9
13 Jun	9	10	11	7.3	0.8	73	39.5
10 Jul	9	12	10	11.1	1.3	133	71.9
20 Jul	11	12	3	15.3	10.3	184	99.5
15 Aug	11	12	3	2.7	1.2	32	17.3
28 Aug	12	12	3	15.7	4.3	188	101.6
14 Sep	10	10	N/A	N/A	N/A	N/A	N/A
2001							
7 Jun	9	11	N/A	N/A	N/A	N/A	N/A
9 Aug	12	12	N/A	N/A	N/A	N/A	N/A

[a] Population estimates of adult cows and yearling bulls: 202 (0.6227 of total *N*) in 1998; 198 (0.6139 of total *N*) in 1999; and 185 (0.6823 of total *N*) in 2000.

[b] Percentage of total estimated adult cows and yearling bulls in Hunt Unit 072 represented through relocation flights. Group representation following some flights represented >100% of estimated adult cow and yearling bull populations. Minimum population estimates provided by Nevada Division of Wildlife.

Table 2. Descriptive statistics for habitat variables in 2.3 km buffers around elk and random locations, Jarbidge Mountains, Nevada, summers 1998–2001. Elk locations were weighted by number of radiocollared cows in each group and represent averages from 136 elk groups on 19 flights. Elk locations were compared to paired, random locations to create a conditional fixed-effects model. Paired *t*-tests evaluated differences in habitat variables between elk group locations and available (random) habitat.

Independent variables	Elk		Random	
	Mean	SE	Mean	SE
Landscape features[a]				
Stream (m)	511.5**	62.7	878.7	94.2
Road (m)	1,920.6**	221.4	2,516.2	236.7
Topography				
Cool Aspect (%)[b]	48.7	1.3	49.9	1.5
Elevation (m)[c]	2,444.1	13.6	2,467.0	16.6
Slope (%)[d]	32.6***	0.5	36.0	0.7
Vegetation Cover (%)				
Aspen	16.3***	0.3	13.7	0.4
Conifer	8.4***	0.6	11.6	0.6
Mahogany	17.1	0.5	17.6	0.6
Sagebrush–herb	54.0	0.9	53.9	1.3
Snowbrush	4.1***	0.2	3.1	0.2

** Elk and random estimates different ($P \leq 0.01$) as tested by paired *t*-test, df = 18.

*** Elk and random estimates different ($P \leq 0.001$) as tested by paired *t*-test, df = 18.

[a] Nearest perennial stream and road to center of elk or random buffer.

[b] Cool aspects are percentage of slopes with N, E, NE, and NW relief in each buffer.

[c] Mean elevation (m) in each buffer.

[d] Mean slope (%) in each buffer.

Table 3. Best model fit statistics for cow elk group summer habitat selection, Jarbidge Mountains, Nevada, 1998–2001. Binary logistic regression modeling compared habitat use of elk cow groups relocated on 19 fixed-wing flights with 19 equal groupings of paired random locations representing habitat availability. Smallest Akaike's information criterion bias-correction for small samples (AIC_c) indicates the most appropriate model for the observed data (Burnham and Anderson 1998).

Model[a]	Parameters	AIC_c	ΔAIC_c
H2O and X2	3	18.290	0.000
H2O and X4	3	32.542	14.252
X2 and X4	3	33.810	15.520
X2 and MAHOG	3	36.444	18.154
X2	2	36.933	18.643
COOL and X2	3	38.706	20.416
ROAD and X2	3	39.040	20.750
X4	2	39.135	20.845
X4 and MAHOG	3	41.109	22.819
COOL and X4	3	41.293	23.003
ROAD and X4	3	41.487	23.197
ROAD and H2O	3	43.744	25.454
H2O and MAHOG	3	44.743	26.453
H2O	2	46.213	27.923
COOL and H2O	3	46.513	28.223
ROAD	2	53.649	35.359
COOL and ROAD	3	54.793	36.503
ROAD and MAHOG	3	55.904	37.614
MAHOG	2	56.579	38.289
COOL	2	56.687	38.397
COOL and MAHOG	3	58.747	40.457

[a] Habitat variables evaluated in each 2.3-km buffer were percentage of cool aspect (COOL), distance (m) from buffer center to the nearest perennial stream (H2O), arcsine square root transformed proportion of mahogany cover (MAHOG), distance (m) from buffer center to the nearest road (ROAD), natural log ratio of aspen to conifer (X2), and natural log ratio of sagebrush to snowbrush (X4).

Table 4. Summer range economic nutritional carrying capacity estimates (I_{NCC}) for 236-kg lactating cow elk, Jarbidge Mountains, Nevada, autumn 1999 and 2000. Estimates reflect nutritional levels for maintenance (2,550 kcal/kg) and optimal (2,750 kcal/kg) animal performance. Original I_{NCC} estimates for each community were adjusted when expected elk densities predicted with resource selection functions (RSFDs) exceeded original I_{NCC} estimates. Differences indicate the influence of predicted habitat use on original estimates. Original I_{NCC} estimates were adjusted to avoid estimates that would promote overuse of forage in communities.

Performance	1999			2000		
	Original	RSFD[a]	Difference[b]	Original	RSFD[a]	Difference[b]
Maintenance						
Aspen	302	392	-90	239	256	-17
Conifer	74	0	74	19	0	19
Mahogany	530	310	220	358	203	155
Sagebrush–herb	1,079	1,740	-661	698	1,137	-439
Snowbrush	548	88	460	341	58	283
Total[c]	2,533	2,530	751	1,655	1,654	456
Adjusted I_{NCC}	1,782			1,199		
Optimal						
Aspen	267	350	-83	164	170	-6
Conifer	20	0	20	5	0	5
Mahogany	468	277	191	332	135	197
Sagebrush–herb	1,001	1,555	-554	283	755	-472
Snowbrush	508	79	429	316	38	278
Total[c]	2,264	2,261	637	1,100	1,098	478
Adjusted I_{NCC}	1,627			622		

[a] Carrying capacity density estimates in each community redistributed with resource selection functions (RSFD).

[b] Differences are predicted RSFD estimates subtracted from original I_{NCC} estimates.

[c] Total I_{NCC} estimates redistributed with RSFDs differ from original I_{NCC} estimates due to rounding error.

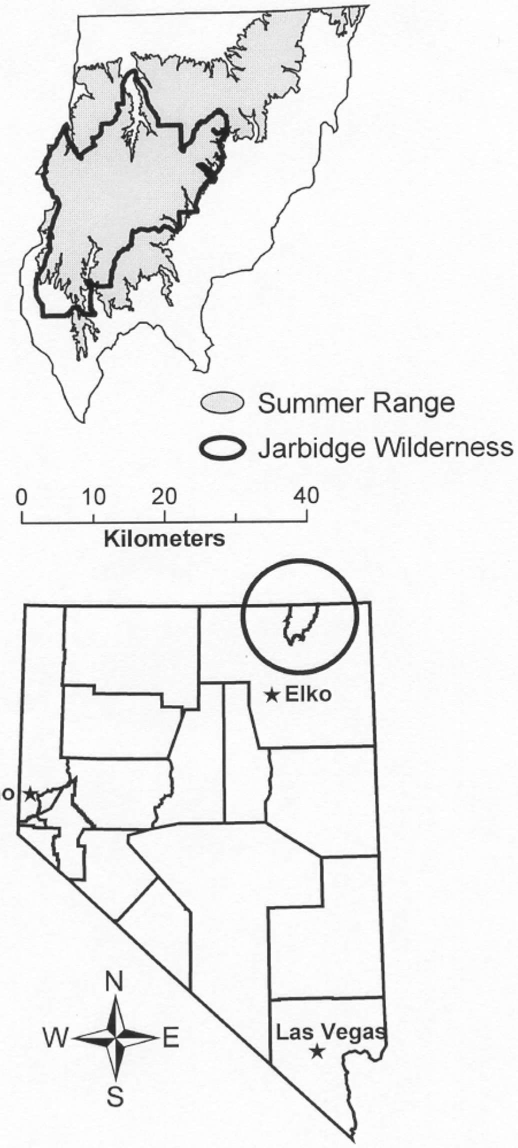


Fig. 1. Elk carrying capacity study area location map, Jarbidge Mountains, Nevada. The study area encompasses the 1,665 km^2 Nevada Division of Wildlife Hunt Unit 072. Summer range was delineated as all area ≥2,135 m and includes 802 km^2. The 392 km^2 U.S. Forest Service Jarbidge Wilderness Area comprises 48.9% of the summer range. Map projection UTM Zone 11; Datum NAD 1927.

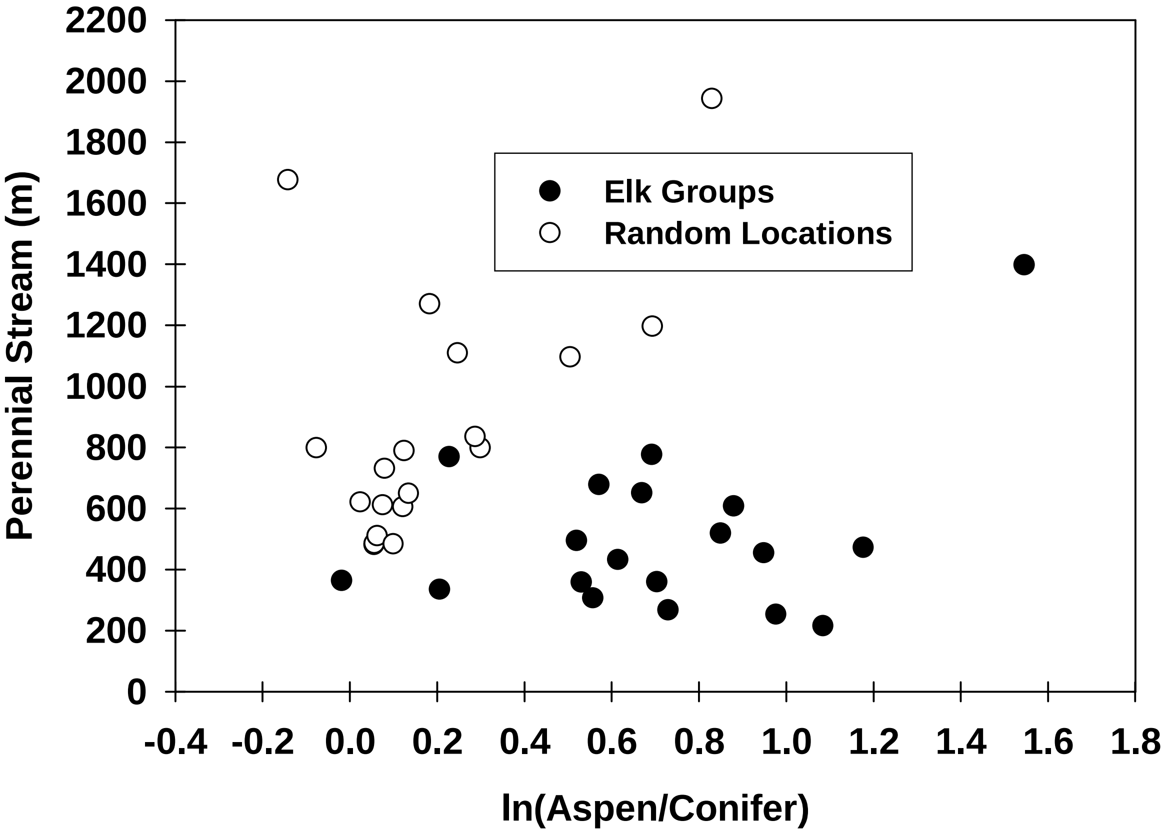


Fig. 2. Bivariate scatter plot between best elk group habitat selection model variables, Jarbidge Mountains, Nevada, 1998–2001. Habitat variables are distance (m) to nearest perennial stream from center of elk and random 2.3-km buffers and the natural log ratio of aspen to conifer in each 2.3-km buffer. Elk group variables were weighted by the number of radio-marked cows in each group on 19 telemetry flights. An equal number of paired, random buffers were evaluated per flight.

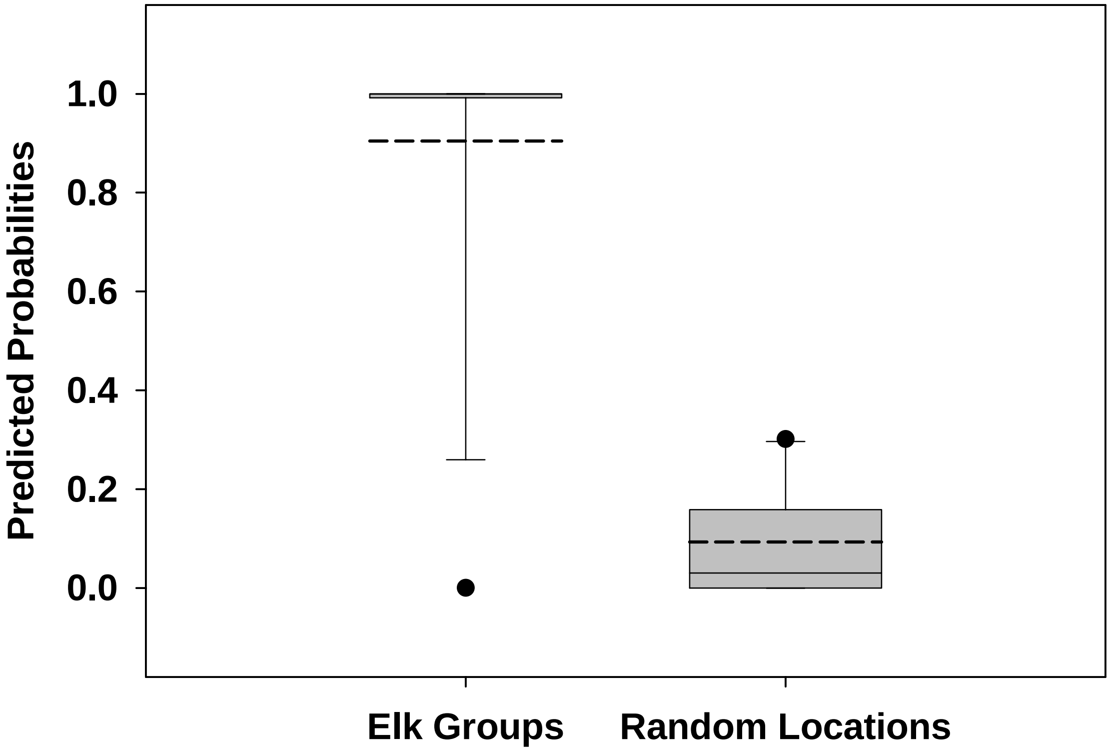


Fig. 3. Boxplots of predicted probabilities of elk presence used in 5-fold cross validation procedures to evaluate performance of cow elk group habitat selection model, Jarbidge Mountains, Nevada, 1998–2001. Medians are solid lines, means are dashed lines, and filled circles are outliers.

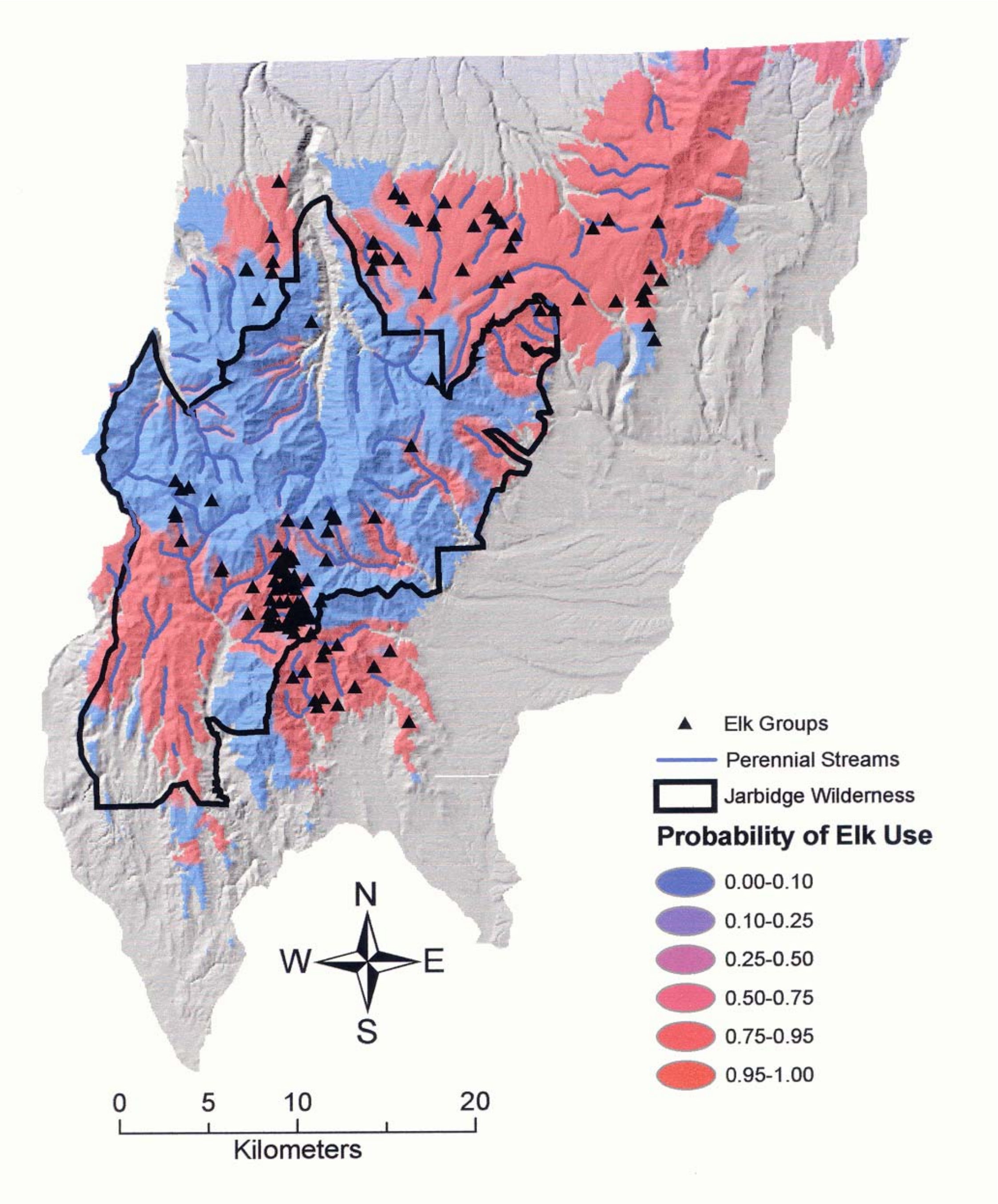


Fig. 4. Probabilities of cow elk group summer range habitat use, Jarbidge Mountains, Nevada, 1998–2001. Highest probabilities of use (0.95–1.00) on this map are the darkest shaded areas on the summer range (light red on colored map). These areas appear lighter than they are depicted in the legend due to a hillshade underlying the probability coverage. Lowest probabilities of use (0.00–0.10) are primarily within the center and northern portions of the Jarbidge Wilderness (light blue on colored map). Map projection UTM Zone 11; Datum NAD 1927.

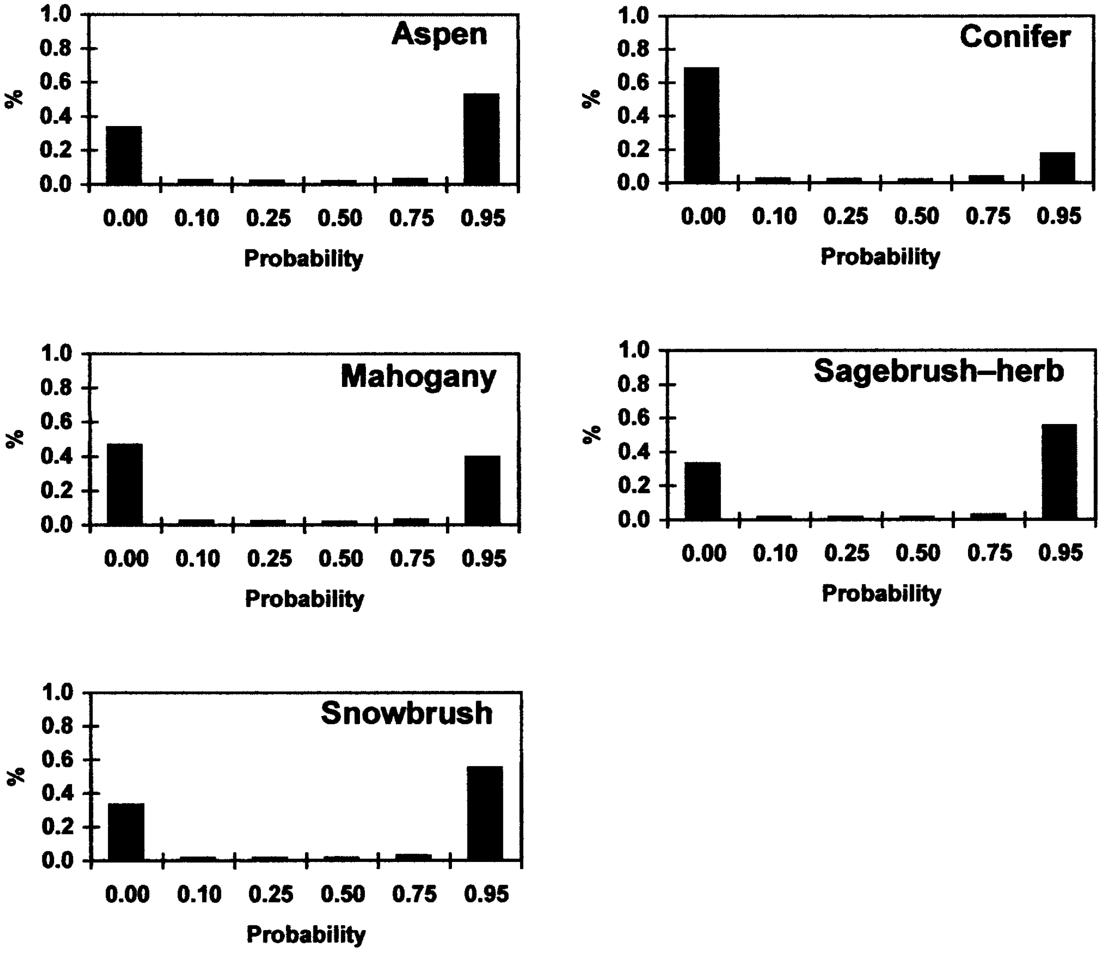


Fig. 5. Proportion of cover types within 6 probability classes of cow elk group habitat use, Jarbidge Mountains, Nevada, 1998–2001. Probabilities were derived through logistic regression modeling and are spatially displayed in Fig. 4.

APPENDIX 1

ELK HABITAT AVAILABILITY MAP: DEVELOPMENT AND ACCURACY ASSESSMENT

OBJECTIVES

Our objectives were to (1) detail the development of an elk habitat availability map based on major vegetative communities in the Jarbidge Mountains of Northeastern Nevada, (2) conduct an accuracy assessment of our map, and (3) report and discuss map results.

METHODS

We created a habitat availability map to represent 5 distinct cover types (aspen, conifer, mahogany, sagebrush, and snowbrush) that characterize study area vegetation and are used by elk in Hunt Unit 072. We obtained three Landsat 7 Enhanced Thematic Mapper (ETM+) images (24 September 1999 [Path 41, Row 31], 15 September 2000 [Path 40, Row 31], and 17 October 2000 [Path 40, Row 31]; Homer et al. 2002). These data have a ground resolution of 30 m (1 pixel = 0.09 ha). We used these Landsat 7 ETM+ scenes to create a habitat availability coverage (map projection, UTM Zone 11; datum, NAD 1927) in ERDAS IMAGINE 8.5 (ERDAS®, Inc., 2801 Buford Highway, NE, Atlanta, Georgia, USA) by: (1) conducting a principal components analysis with the original data to reduce the dimensionality of the data from 6 bands to 3, (2) performing an unsupervised classification on the principal components image, and (3) masking and merging the 3 classified images to produce one continuous map without cloud and shadow. All images used to create the final map were reclassified into 7 cover types (aspen, conifer, hayfields, mahogany, rock, sagebrush, and snowbrush) in ERDAS IMAGINE 8.5 with 114 ground-control points collected in 2000. A reclassified Nevada GAP (Scott et al. 1993) vegetation coverage and USGS 7.5 minute topographic maps were also consulted to classify pixels. We further reclassified these data into the 5 major cover types in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA) by combining rock with conifer and hayfields with sagebrush due to their small extent and juxtaposition and interspersion with conifer and sagebrush.

We evaluated map accuracy within 100-m buffers around 125 livestock and wildlife locational ground points collected with a GPS unit in the study area in 1998. Buffer size represented error (± 100 m) of 1998 points due to the United States Department of Defense selective availability degradation system operational at that time (Clarke 1999). We intersected error buffers in ArcView 3.2 with vegetation in the study area to obtain the area of the 5 major cover categories within each buffer. We used compositions of cover types in each buffered area around each location to evaluate accuracy of the habitat map. Map points were correctly classified if the cover recorded from ground was present within the buffer. We assessed map accuracy by constructing a table to evaluate overall map accuracy (total number correctly classified points ÷ total number of points evaluated) and two types of model error (error of omission and error of commission). Omission error represents points where a cover type was detected from the ground, but not from the availability map (% omission = omission ÷ [number of points predicted by map and detected from ground (correct present) + omission). Commission error corresponds to points predicted by the habitat map, but not detected from the ground (% commission = commission ÷ [correct present + commission]).

RESULTS AND DISCUSSION

The area ≥2,135 m was defined as summer range because 91.3% (136 of 149) of radio-marked elk groups relocated in summers on fixed wing flights occurred in this elevational zone (Fig. 1). Cover type composition for the summer range from reclassified Landsat 7 ETM+ data was 15.1% aspen, 10.7% conifer, 19.7% mahogany, 51.8% sagebrush, and 2.7% snowbrush (Table 1). Overall, the composition of summer range consisted of more forested habitats and less sagebrush compared to the entire study area (Table 1; Fig. 2). We detected 89.6% map accuracy within 100-m buffers around 125 points classified from ground in 1998 (Table 2). Highest omission error for individual cover types was for conifer (57.1%), while sagebrush (91.5%) was lowest (Table 2).

A principal assumption of habitat use-availability studies is that availability remains constant over the period of study (Alldredge et al. 1998, Erickson et al. 2001). A 12,141 ha fire on the eastern slope of the Jarbidge Mountains occurred in early August 2000. Most of the burned area was at elevations <2,135 m and in sagebrush. This fire did not change overall summer habitat composition, and the distribution of summer telemetry locations after this date did not change from previous summer locations.

In northern Nevada, 80% of aspen stands occur at 1,981–2,347 m (modal elevation = 2,070 m), typically in moist sites or where snow accumulates (Mueggler 1988). Snowbrush grows adjacent to or in aspen in snowbank associations throughout the study area. Furthermore, spectral reflectance for snowbrush and aspen is similar. Thus snowbrush composition, although it only comprised 2.6% of the area above 2,135 m, likely reflected association with aspen. However, map accuracy assessments show neither species was misclassified as the other species (Table 2).

LITERATURE CITED

Alldredge, J.R., D.L. Thomas, and L.L. McDonald. 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:237–253.

Clarke, K.C. 1999. Getting started with geographic information systems. Second edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Erickson, W.P., T.L. McDonald, K.C. Gerow, S. Howlin, and J.W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pages 209–242 *in* J.J. Millspaugh, and J.M. Marzluff, editors, Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Homer, C., C. Huang, L. Yang, and B. Wylie. 2002. Development of a circa 2000 land cover database for the United States. In 2002 American Society for Photogrammetry and Remote Sensing–American Congress on Surveying and Mapping Annual Conference and FIG XXII Congress Proceedings, April 19–26, Washington, D.C.

Mueggler, W.F. 1988. Aspen community types in the Intermountain Region. U.S. Forest Service, General Technical Report, INT-250.

Scott, J.M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, et al. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monograph No. 23.

U.S. Forest Service. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. U.S. Forest Service, Humboldt National Forest, Elko, Nevada.

Table 1. Cover type availability in the study area, Nevada Division of Wildlife Hunt Unit 072 and summer range, the area in Hunt Unit 072 ≥2,135 m, Jarbidge Mountains, Nevada.

	Study area		Summer range	
Cover	Area (ha)	%	Area (ha)	%
Aspen	16,350	9.8	12,120	15.1
Conifer	9,287	5.6	8,581	10.7
Mahogany	22,015	13.2	15,828	19.7
Sagebrush	116,432	69.8	41,490	51.8
Snowbrush	2,743	1.6	2,140	2.7
Total[a]	166,827		80,159	

[a] Total areas differ from study area sizes due to differences in data coverages.

Table 2. Map accuracy of Landsat 7 ETM+ reclassified data within 100-m buffers around 125 wildlife and livestock location points classified from ground, summer 1998, Jarbidge Mountains, Nevada.

	Ground vegetation classification						Commission		
Map vegetation	Aspen	Conifer	Mahogany	Sagebrush	Snowbrush	Grand total	Error	%	User accuracy
Aspen	15		1	3		19	4	21.1	79.0
Conifer		3		1		4	1	25.0	75.0
Mahogany		1	8			9	1	11.1	88.9
Sagebrush	2	3	1	75	1	82	7	8.5	91.5
Snowbrush					11	11	0	0.0	100.00
Total	17	7	10	79	12	125			
Omission error	2	4	2	4	1	13			
Error %	11.8	57.1	20.0	5.1	8.3	10.4			
Producer's error	88.2	42.9	80.0	94.9	91.7	89.6			
Map accuracy (%)	89.6								

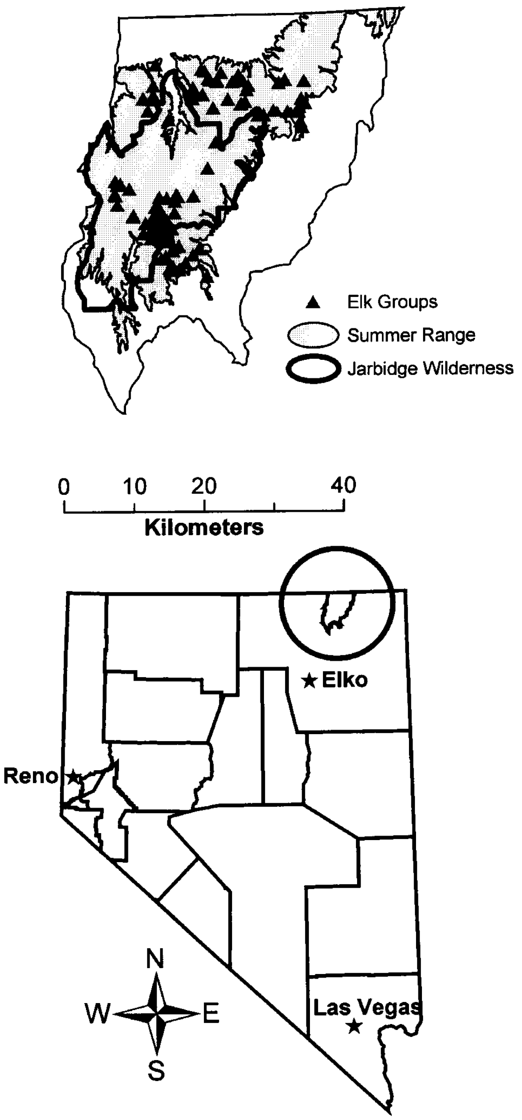


Fig. 1. Elk carrying capacity study area location map overlain with 136 cow elk group locations, Jarbidge Mountains, Nevada, 1998–2001. The area $\geq$2,135 m was defined as summer range because 91.3% (136 of 149) of radio-marked elk groups relocated in summers on flights occurred in this elevational zone. Summer range includes 48.2%, or 802 km^2 of the 1,662-km^2 study area. The 392 km^2 U.S. Forest Service Jarbidge Wilderness Area comprises 48.9% of the summer range. Map projection UTM Zone 11; Datum NAD 1927.

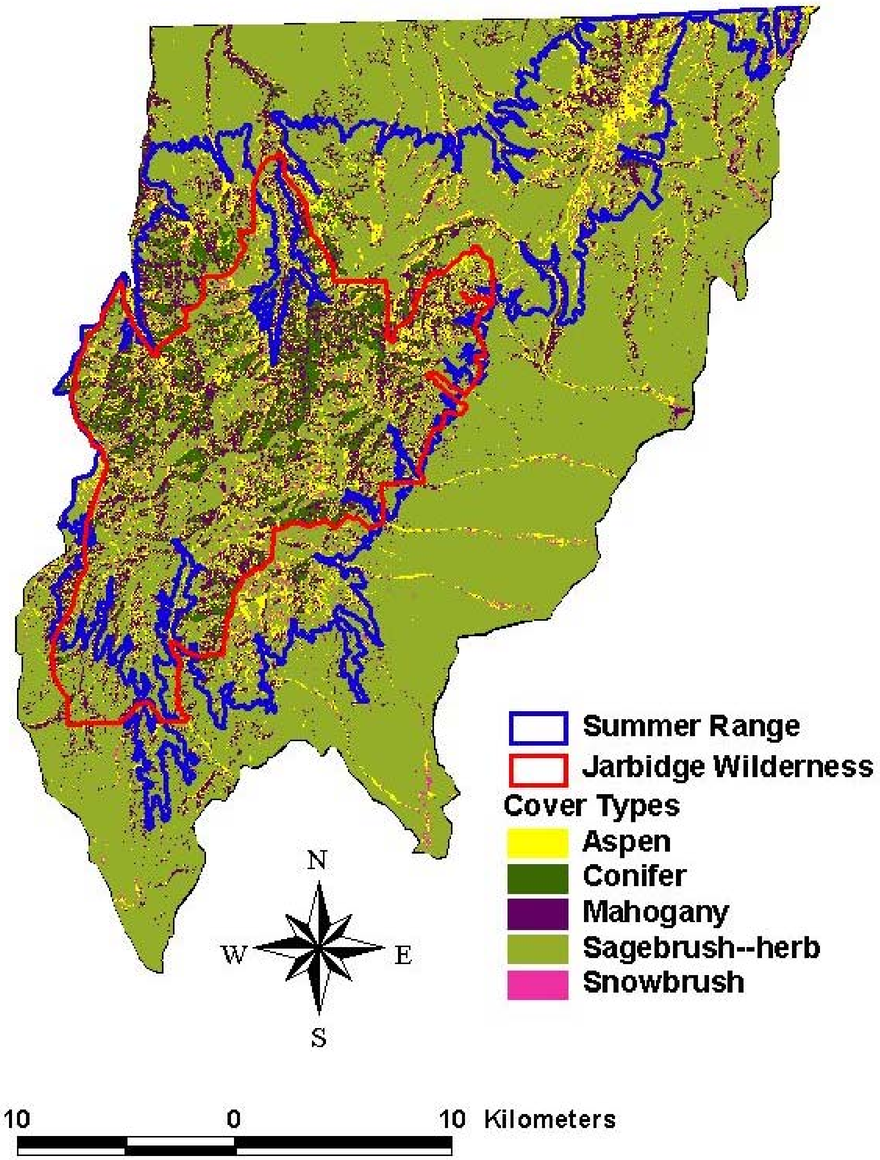


Fig. 2. Cover type availability map, Jarbidge Mountains elk carrying capacity study area, 1998–2001. Map projection UTM Zone 11; Datum NAD 1927.

APPENDIX 2

SUMMER NUTRITIONAL CARRYING CAPACITY MODEL FOR ELK IN THE JARBIDGE MOUNTAINS, NEVADA

Ungulate nutritional carrying capacity model parameters include (1) consumable forage available, (2) amount of the limiting nutrient or nutrients in consumable forage, (3) the gender, age, and nutrient demand of the animals modeled, and (4) the season and length of time animals will forage under these conditions (Mautz 1978, Hobbs et al. 1982). This appendix describes the development of an elk (*Cervus elaphus*) nutritional carrying capacity model for summer range in northeastern Nevada. Our carrying capacity and variance estimators appear first and are then followed by 5 sections that define and detail major portions of our nutritional carrying capacity predictive model. Methods and pertinent results are reported in each section, and, where needed, we provide introductory explanations. Carrying capacity estimates are reported in Chapter 5. Section I (pages 143–152) covers derivation of standing digestible energy (SDE [kcal/ha]), the currency for my model. Section II (pages 153–156) details estimates of use of SDE by elk. Section III (pages 157–159) describes the area available to elk in each community. Section IV (pages 159–160) provides information on dry matter intake and digestible energy required for 236-kg lactating cow elk, the modeled animal. Section V (pages 160–161) discusses the delineation of the limiting autumn period using climatic data.

NUTRITIONAL CARRYING CAPACITY MODEL

We developed the following predictive model to estimate economic nutritional carrying capacity (I_{NCC}) at maintenance performance (2,550 kcal/kg forage) and optimal performance (2,750 kcal/kg forage; Cook et al. In Press). We calculated SEs as the square root of the variance for I_{NCC} for each year (i), and 95% CIs as $I_{NCCi} \pm t_{\alpha/2,\, n-1} \times \mathrm{SE}$.

$$\widehat{I_{NCCi}} = \sum_{j=1}^{n}\sum_{m=1}^{5} \frac{\widehat{SDE_{jm}} * \widehat{Use_{jm}} * Area_{jm}}{DMI * DER * Days_i}$$

where

$\widehat{I_{NCCi}}$ = Economic nutritional carrying capacity in autumn of year i,

SDE_{jm} = Mean standing digestible energy (kcal/ha) for forage item j in cover type m,

Use_{jm} = Proportion of forage item j eaten by elk in cover type m,

$Area_{jm}$= Area (ha) of forage item j in cover type m,

DMI = Dry matter intake (kg/day),

DER = Digestible energy required (kcal/kg), and

$Days_i$ = Number of days of autumn in year i.

Variance for the estimator $\widehat{I_{NCCi}}$ was approximated as the variance of a product (Goodman 1960):

$$\widehat{V_{I_{NCCi}}} = \sum_{j=1}^{n}\sum_{m=1}^{5} C_{jm}^{2}\left(\hat{V}\left[(\widehat{SDE}_{jm})(\widehat{Use}_{jm})\right]\right)$$

where

$$C_{jm}^{2} = \left(\frac{Area_{jm}}{(DMI * DER * Day_i)}\right)^{2}$$

and,

$$\hat{V}\left[(\widehat{SDE}_{jm})(\widehat{Use}_{jm})\right] = \left(\widehat{SDE}_{jm}^{2}\right)\left(\hat{V}(\widehat{Use}_{jm})\right)+\left(\widehat{Use}_{jm}^{2}\right)\left(\hat{V}(\widehat{SDE}_{jm})\right)+\left(\hat{V}(\widehat{SDE}_{jm})\right)\left(\hat{V}(\widehat{Use}_{jm})\right)$$

I. STANDING DIGESTIBLE ENERGY

Introduction

An important consideration in my study was to compute elk carrying capacity while incorporating forage consumed by cattle, domestic sheep, mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) sharing summer range with elk on 11 domestic sheep, 27 cattle, and 1 common use summer and early fall grazing allotments. We accounted for forage used by other ungulates in my model by calculating carrying capacity with residual forage in autumn following livestock grazing in conjunction with use by other herbivores. Residual forage represented the potential forage needs of other ungulates in relation to a population of approximately 300 elk that inhabited the Jarbidge Mountains during my study (Chapter 1).

In our study, evaluation of digestible energy (DE), crude protein, and macrominerals including calcium, magnesium, phosphorous, potassium, sodium (Na), and sulfur in common elk forages indicated DE was probably the most limiting nutrient. Woody browse was the only forage that met DE requirements for lactating 236-kg cow elk in early fall (Chapter 4). Sodium was very deficient in range forages in my study area, but we do not consider it to be a limiting nutrient because: (1) as a rule, Na in plants other than in halophytes does not meet animal requirements (Kincaid 1988, Robbins 1993), and (2) grazing animals in spring and summer compensate for low Na by visiting mineral springs, mineral licks, and livestock salt placements to ingest salty water and salt-impregnated soils (Bechtold 1996, Beck et al. 1996). Energy is a very useful nutrient to model nutritional carrying capacity because the energy fraction in forages is highly correlated with content of other important nutrients including protein (Vallentine 1990).

We selected a 236-kg cow elk with calf at side lactating through mid-autumn and with average dry matter intake (DMI), activity, and metabolic demands as my model animal to calculate nutritional carrying capacity for 1999 and 2000 (Cook 2002). Elk nutritional requirement calculations have typically considered 236 kg to be an average size for elk cows (Nelson and Leege 1982, Cook 2002). Forage quantity and quality suitable to cow elk needs are directly related to elk population productivity, as energetic needs of lactating cow elk in summer are 2 or 3 times higher than during gestation (Robbins 1993).

We used the product of DE (kcal/kg) and standing crop (kg/ha) to represent standing digestible energy (SDE; kcal/ha) of key forage species. Specifically, we calculated SDE for perennial forbs and perennial graminoids in aspen (*Populus tremuloides*), conifer, curlleaf mountain mahogany (*Cercocarpus ledifolius*), and sagebrush (*Artemisia* spp.)–herb communities and aspen in aspen communities, mahogany in mahogany communities, and snowbrush ceanothus (*Ceanothus velutinus*) in snowbrush communities. Mountain snowberry (*Symphoricarpos oreophilus*) represented the shrub component selected by elk in aspen, conifer, mahogany, and sagebrush–herb communities. Our purpose in estimating carrying capacity based on availability of SDE in key forages was two-fold: (1) proper use of key forages in key foraging areas generally indicates proper use of rangeland grazing units (Holechek 1988), and (2) key forage species are common forage items that comprise the bulk of ungulate diets in a grazing area (Holechek et al. 1989).

We identified 12 key forage species in the study area through fecal and feeding site evaluations (see Chapter 3; Hobbs and Spowart 1984). Key forage species included 2 forbs: arrowleaf balsamroot (*Balsamorhiza sagittata*) and spurred lupine (*Lupinus caudatus*); 6 grasses: bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca* *idahoensis*), Kentucky bluegrass (*Poa pratensis*), mountain brome (*Bromus marginatus*), needlegrass (*Achnatherum* spp.), and Sandberg bluegrass (*Poa secunda*); and 4 woody species: aspen, curlleaf mountain mahogany, mountain snowberry, and snowbrush ceanothus. Those forage species prevalent in each community were grouped by forage categories and DE content averaged to represent energy content of key forages in each community. Calculating SDE required me (1) to estimate standing crop of key forage categories and species in aspen, conifer, mountain mahogany, sagebrush–herb, and snowbrush communities and (2) to approximate DE for key forage items in each of these communities. The following sections detail my sampling methodology, statistical analyses, and relevant results.

Standing Crop Estimate Methods

Aspen, Mahogany, and Snowbrush Community Standing Crop Plots.—In 1999, we placed 1 225-m^2 plot in aspen and mahogany communities in the Black Spring, Spring Creek, and Wilson Creek cattle allotments. A mahogany plot was placed in the Pole Creek allotment instead of the Spring Creek allotment in 1999. Snowbrush community plots consisted of 2 parallel, 75-m lines spaced 5 m apart and were placed in the Black Spring, Spring Creek, and Wilson Creek grazing allotments. We placed 1 additional transect in aspen, mahogany, and snowbrush communities in 2 additional allotments (Caudle Creek and Pole Creek or Spring Creek) in 2000. Our sampling effort thus included 3 community plots in 3 allotments ($n = 9$) in 1999 and 3 community plots in 5 allotments ($n = 15$) in 2000.

Distinct allotments facilitated interspersion of experimental units (Hurlbert 1984). We strategically placed community plots in patches (1) under similar topographic conditions, (2) to represent the vegetative understory typifying each allotment, (3) where prior livestock and elk sign indicated both species were likely to forage, and (4) that were large enough to facilitate plot placement. Standing crop plots provided seasonal productivity estimates for annual forbs, perennial forbs, perennial graminoids, and woody browse in key communities. Each sampling plot was grazed each year by the end of the grazing season.

Aspen, Mahogany, and Snowbrush Community Standing Crop Sampling.—Surveyor tapes placed in aspen and mahogany community plots delineated 10 perpendicular lines spaced 1.5 m apart along a 15.24-m center baseline. Ten locations for sampling plots were spaced equidistantly in 1.5 m intervals along each of these lines for a total of 100 possible sampling plot locations. Snowbrush community plots were marked at 1.0 m and then again at each 1.5 m position along parallel lines demarcated with surveyor tapes to provide a possibility of 50 sampling locations along each 75-m baseline. Repeated sampling occurred at each community plot during early summer (late June), mid-summer (early August), and early fall (late September–early October) 1999 and 2000. Snowbrush was first sampled in mid-summer 1999, but was only evaluated from early fall 1999 through early fall 2000 due to mid-summer 1999 over-estimating bias.

We employed a double sampling technique to measure biomass in nested quadrats (Bonham 1989, Interagency Technical Reference 1996). We evaluated herbs and woody browse current annual growth (CAG) at aspen and mahogany community plots, while only woody browse was evaluated at snowbrush community plots because herbs were a very minor component of snowbrush communities. Each nested quadrat consisted of a 0.1-m^2 (20 x 50 cm) herbaceous quadrat nested along the bottom center of a 1.0-m^2 woody browse quadrat. Restriction of randomization excluded quadrats clipped at earlier sampling periods to reduce bias. We ocularly estimated biomass by species or forage class in each of 15

(1999) or 20 (2000) nested quadrats randomly distributed among sampling locations within each 225-m^2 community plot. At each sampling occasion we randomly selected 3 (1999) or 4 (2000) sampling quadrats from the 15 or 20 nested quadrats and clipped all herbaceous phytomass and woody browse CAG lying within each nested sampling quadrat from ground level to a height of 2 m to simulate elk foraging reach. Fresh weights were recorded to the nearest 0.5 g and weights less than 0.5 g (traces) were recorded as 0.1 g.

Linear regressions using estimated fresh forage class weights as independent variables and clipped weights as dependent variables (PROC REG; SAS Institute 2001) at nested quadrats at each community in each sampling period were used to calibrate estimates of fresh standing crop in quadrats that were not clipped. We pooled fresh weights within communities and among allotments when the number of samples was <8 per allotment in any sampling period. Clipped samples were placed in paper bags and initially air-dried to prevent degradation, then oven dried in a forced-air oven at 60 ºC for 24 hr and weighed to ± 0.01 g. Mean % DM from clipped quadrats at each community was multiplied by calibrated estimates of fresh herbage in estimated quadrats to calculate g DM/m^2 for ocularly estimated quadrats. Seasonal g DM/m^2 were averaged at each community-sampling plot from g DM in all nested quadrats.

Aspen, Mahogany, and Snowbrush Standing Crop Statistical Analyses.—My experimental design was a randomized complete block (whole plot) with repeated measures over 2 years and 3 seasons (split plot). We compared herbs in aspen and mahogany communities with ANOVA's. Woody browse standing crop was only compared within communities at each time period because woody browse compositions were not comparable between communities. Blocks were allotments and treatments were community (for aspen and mahogany herbs) and time period. Fixed effects were time period and community; allotment and allotment × community interactions for herbaceous comparisons were random effects. I used Akaike's information criterion (AIC) to determine whether autoregressive, autoregressive moving average, compound symmetric, or heterogeneous autoregressive time series covariance structures best fit these data; the covariance structure with the lowest AIC value was selected (Burnham and Anderson 1998).

I conducted transformations (square root and log10) of standing crop responses if they did not meet assumptions of statistical tests (Oehlert 2000). Two annual forb observations and 1 snowberry observation in the aspen community analysis were outliers and removed because of their large influence on equal variance and normality. Removing these outliers did not change statistical significance of the Type III global *F*-test. Differences were evaluated with ANOVA (PROC MIXED; SAS Institute 2001) within community (aspen, mahogany, and snowbrush), time period, and for the community × time period interaction. The main effect of time was only considered in ANOVA models evaluating standing crop of woody browse species. Estimated treatment response least squares means were back-transformed (Fowler et al. 1998). Standard errors associated with transformed least squares means were approximated to their original scale according to the delta method (Bishop et al. 1975). Reported standing crop estimates are accordingly back-transformed lsmeans ± 1 SE. Post hoc multiple comparisons were conducted with the Tukey-Kramer HSD test to assess pairwise differences in forage class phytomass among communities, time period, and community × time period interactions. Statistical significance was set at $\alpha = 0.05$.

Conifer and Sagebrush Community Standing Crop Estimates.—I obtained DM forage production information for conifer and sagebrush–herb communities from other sources

(Jensen et al. 1988, U.S. Forest Service 1988). I retrieved forb, graminoid, and mountain snowberry data from each data source to represent composition of available elk forages in both community types. Although annual forbs were included in the forb component of sagebrush–herb communities, they represented a negligible portion of those estimates. Feeding sites and microhistological fecal analysis indicated elk only incidentally selected sagebrush and other common shrubs such as viscid rabbitbrush (*Chrysothamnus viscidiflorus*), and sub-shrubs that elk did occasionally select such as whorled buckwheat (*Eriogonum hieracaloides*) were evaluated as forbs in both papers. Mountain snowberry provided a good representation of woody forage available to elk because it was occasionally selected by elk and was the most ubiquitous woody browse species among all communities.

Conifer data were summarized from 3 subalpine fir (*Abies lasiocarpa*) communities on the Pole Creek bench in the northern portion of the study area in October 1985 (U.S. Forest Service 1988). Snow water equivalents on 1 April 1985 at the Pole Creek SNOTEL site were 566 mm, or 108.3% of normal, similar to snowpack water conditions in 1999 and 2000. This precipitation index suggests forage production should have been near normal during 1985 on the Pole Creek bench. Forage production values in 8 sagebrush community types in northeastern Nevada, also common to the Jarbidge Mountains, were averaged to obtain mean production values for each forage category across the sagebrush-herb complex (Tables 2, 4, and 6 in Jensen et al. 1988). Sagebrush communities on the Pole Creek bench evaluated in October 1985 were included in Jensen et al.’s (1988) study (M. E. Jensen, U. S. Forest Service, personal communication, 2002). I adjusted standing crop to reflect livestock consumption in conifer and sagebrush–herb communities because researchers evaluated forage standing crop in early fall in areas with very light grazing (M. E. Jensen, U.S. Forest

Service, personal communication, 2002). Adjustments were based on Humboldt-Toiyabe National Forest allowable use levels for non-riparian rangeland of 60% for herbs and 50% for CAG of shrubs in deferred rotation allotments.

Standing Crop Results

Herbaceous Standing Crop in Aspen and Mahogany Communities.—I detected significant differences in annual forb standing crop between aspen and mahogany communities ($F_{1,4} = 33.34$, $P = 0.005$), time period ($F_{5,26} = 47.28$, $P < 0.001$), and the community × time period interaction ($F_{5,26} = 157.76$, $P < 0.001$). Among years, aspen communities contained higher annual forb standing crop than mahogany communities in early summer and mid-summer, but did not differ in early fall (Table 1). I detected significant differences in perennial forb standing crop between aspen and mahogany communities ($F_{1,4} = 8.98$, $P = 0.040$), time period ($F_{5,28} = 27.61$, $P < 0.001$), and the community × time period interaction ($F_{5,28} = 3.58$, $P = 0.013$). Aspen communities contained seasonally higher perennial forb standing crop than mahogany communities both years; however, seasonal perennial forb standing crop did not differ significantly between communities during some seasons (Table 1). There was no difference in perennial graminoid standing crop between aspen and mahogany communities, while time period ($F_{5,28} = 3.65$, $P = 0.012$) and the community × time period interaction ($F_{5,28} = 3.38$, $P = 0.016$) did differ. Differences were less pronounced for perennial graminoid standing crop between time periods than for perennial or annual forbs in aspen and mahogany communities (Table 1). Across both years, herbaceous standing crop was lowest in early fall (Table 1).

Woody Browse Standing Crop in Aspen, Mahogany, and Snowbrush Communities.—We did not detect a difference in snowbrush standing crop among time periods, but did detect aspen ($F_{5,14} = 5.30$, $P = 0.006$) and mahogany ($F_{5,14} = 7.94$, $P = 0.001$) time period differences for CAG standing crop (Table 2). More aspen and mahogany CAG were available in early fall 2000 than in early fall 1999 (Table 2). There was no difference in mountain snowberry in aspen communities among time periods, but there was a significant difference for mountain snowberry CAG among time periods in mahogany communities ($F_{5,14} = 13.05$, $P < 0.001$). There was less snowberry CAG standing crop in mahogany communities in early summer and mid-summer 1999 than in early summer and mid-summer 2000, respectively. There was no difference in snowberry standing crop in mahogany communities in early fall 1999 and 2000 (Table 2).

Herbaceous Standing Crop in Conifer and Sagebrush–herb Communities.—Herbs in sagebrush–herb communities in autumn 1985 were typically higher than in aspen and mahogany communities in 1999 and 2000 (Tables 1 and 3). Herbs in conifer communities were substantially lower than in aspen, mahogany, and sagebrush–herb communities in early fall (Tables 1, 3, and 4). Snowberry standing crop was similar in aspen, mahogany, and sagebrush–herb communities in early fall and was much higher than in conifer communities in early fall (Tables 2, 3, and 4).

Energy Content of Forage

Mean digestible energy (kcal/kg) calculated in early fall 1999 and 2000 for perennial forbs, perennial graminoids, and woody browse composing each community represented energy content in forages during autumn (see Chapter 4). Annual forbs were excluded from energy calculations because they were not an important dietary component (see Chapter 3) and their abundance may reflect herbage composition resulting from excessive grazing. Energy content of arrowleaf balsamroot and spurred lupine were averaged to represent perennial forb energetic value for all communities. Mean DE for major woody browse species in each community was calculated on a species-specific basis. Woody browse species evaluated for DE content were aspen and mountain snowberry in aspen communities, curlleaf mountain mahogany and mountain snowberry in mahogany communities, snowbrush ceanothus in snowbrush communities, and mountain snowberry in sagebrush–herb and conifer communities. Kentucky bluegrass, mountain brome, and needlegrass DE were averaged to represent grass energy in aspen communities. Bluebunch wheatgrass, mountain brome, and needlegrass DE were averaged to represent energy content in grasses in conifer and mahogany communities. Digestible energy in bluebunch wheatgrass, Idaho fescue, Kentucky bluegrass, mountain brome, needlegrass, and Sandberg bluegrass were averaged to calculate mean energetic content in grasses across the sagebrush–herb complex.

Standing Digestible Energy

Standing digestible energy (kcal/ha) was calculated as the product of mean DE (kcal/kg) and mean residual standing crop (kg/ha) for each forage category in each community. My approach of evaluating standing crop ensured carrying capacity calculations do not promote overuse of sensitive communities while providing forage to livestock and other wild ungulates sharing summer range with elk.

II. STANDING DIGESTIBLE ENERGY USED BY ELK

Elk Feeding Site Sampling Methods

Systematic flights to relocate collared cow elk groups were conducted during summers 1999 and 2000 by J. Williams, an NDOW wildlife biologist. Universal Transverse Mercator coordinates for elk locations were provided to my field crew to facilitate locating elk on the ground. To bolster feeding site samples, we included radio-telemetry relocations and general observations of cow elk groups. Feeding site locations were categorized as those located from June until before (spring) or after (summer) livestock stocking on 10 July. We located elk until mid-September when antlerless elk hunting seasons began.

We employed focal animal sampling to randomly select individual elk from groups on the ground (Altmann 1974) to determine locations for feeding site placement. We considered feeding sites to be areas where focal elk were observed foraging undisturbed for at least 15 min. We selected 2 feeding sites when elk groups were distributed between 2 distinct and adjacent community types (Irwin and Peek 1983). A crude map was sketched for each feeding site to guide field workers back to exact elk group locations to conduct sampling. Feeding sites used by other ungulates were eliminated due to dual use biases, which allowed consideration of elk-only use in feeding sites (Irwin and Peek 1983). We examined feeding sites within 1 week from observations to reduce forage regrowth biases.

A 100-m^2 macroplot delineated by an assembly of cords extended in the 4 cardinal directions was placed on the center of each feeding site. Ten (1999) or 15 (2000) nested plots consisting of 1 0.1-m^2 herbaceous and 1 1.0-m^2 shrub plot at each location were placed within the macroplot at previously determined positions. Percentage of estimated use and estimated residual standing crop were ocularly estimated. Herbaceous phytomass and shrub

CAG were evaluated to a height of 2 m from the ground to account for elk foraging reach. Double sampling (Bonham 1989) was employed in each feeding site to reduce sampling effort. Two (1999) or 3 (2000) of the plots were randomly selected and all of the standing crop within each plot was clipped. Procedures for handling clipped fresh weight samples, computation of linear regression correction factors, and calculation of g DM/m^2 standing crop mirror those described elsewhere in this appendix.

Elk Feeding Site Statistical Analyses

My experimental design was completely randomized with community and time period as main effects. We categorized use of DM within feeding sites according to forage classes including annual forbs, perennial forbs, perennial graminoids, and woody browse. Forage class proportionate use data were arcsine square root transformed (Fowler et al. 1998) to meet assumptions of normality and equal variance prior to statistical testing. One perennial graminoid observation was considered an outlier and removed because of its large influence on equal variance and normality. Removing this outlier had no effect on statistical significance. Feeding sites were classified as forested (aspen and mahogany), or sagebrush–herb (sagebrush and meadows) and were further classified as spring (before livestock entry) or summer (after livestock entry) and according to year of observation. In each case, community × time period was a non-significant interaction term and was pooled into ANOVA model sampling error. Forested and sagebrush–herb community data were pooled across years and seasons, as there was no difference between seasons or years (Tukey-Kramer HSD tests, $P > 0.05$). We used 1-way ANOVA (PROC GLM; SAS Institute 2001) to evaluate differences between sagebrush–herb and forested communities. Feeding site use estimates by forage class in communities are reported as raw estimates ± SE. Statistical significance was set at $\alpha = 0.05$.

Elk Feeding Site Results

I sampled 13 sagebrush–herb and 9 forested elk feeding sites in 1999 and 10 sagebrush–herb and 5 forested elk feeding sites in 2000. I detected no difference in use between sagebrush–herb and forested communities for each forage category (Fig. 1). Estimated elk use in forested communities was 10.1 ± 2.9% (mean ± SE), 4.5 ± 2.2%, and 0.9 ± 0.3% for perennial forbs, woody browse, and perennial graminoids, respectively. And in sagebrush–herb communities, estimates were 9.1 ± 1.8%, 3.5 ± 1.7%, and 1.3 ± 0.3% for perennial forbs, woody browse, and perennial graminoids, respectively. Annual forb use was probably mainly incidental to other herbivory as use was only 0.5 ± 0.4% and 0.3 ± 0.3% in forested and sagebrush–herb communities, respectively. In my model, feeding site use percentages were converted to proportions and multiplied by SDE estimates to provide a realistic estimate of the quantity of each forage item elk could consume. Use estimates were further modified below.

Standing Digestible Energy Adjustment to Account for Differential Nutrient Contents

When calculating nutritional carrying capacity, Hobbs and Swift (1985) advocated incorporating the quality of diets obtainable by populations in specific habitats because dietary quality is often inversely related to its abundance in many ecosystems. Hobbs and Swift (1985) provided an algorithm to calculate carrying capacity for mule deer and bighorn sheep (*Ovis canadensis*) in burned and unburned mountain shrub habitat in Colorado. Dry matter, nitrogen, and metabolizable energy of plants and plant parts consumed by these herbivores were quantified within habitats and for differing levels of diet quality. Carrying capacity was then predicted based on nutrient abundance divided by animal requirements considered in diets with different levels of nutrient concentrations. In this context, nutritional carrying capacity better approximated the ability of habitats to provide for the biological requirements of animals than the more arbitrary division of range nutrient supply by animal requirements. This procedure has been widely applied to model carrying capacity for a variety of ungulates (Cook 1990, McCall et al. 1997, DeYoung et al. 2000)

We used Hobbs and Swift's (1985) algorithm to adjust the amount of forage likely to be mixed in diets of foraging elk selecting maintenance and optimal performance diets (Cook et al. In Press). We accordingly proportionally adjusted the variance of each proportionally adjusted I_{NCC} estimate. These adjustments constrained my model downward by removing low quality forage (Hobbs and Swift 1985). Perennial graminoids in aspen, conifer, and sagebrush–herb communities in 1999 and 2000 and in mahogany in 2000 were removed from I_{NCC} estimates after the algorithm indicated SDE content was too low to provide a mixed diet meeting cow elk requirements for maintenance performance in autumn. Perennial graminoids were likewise removed from autumn 1999 and 2000 I_{NCC} estimates in aspen, conifer, mahogany, and sagebrush–herb communities because they did not provide energy sufficient to meet cow elk requirements for optimal performance.

III. SUMMER HABITAT AVAILABILITY

Habitat Area Available on Elk Summer Range

We delineated all area ≥2,135 m as elk summer range because 91.3% of cow elk groups relocated on telemetry flights across summers 1998–2001 were found in this region. Summer range includes 48.1%, or 80,159 ha of the study area. Aspen covered 12,120 ha (15.1%), conifer 8,581 (10.7%), curlleaf mountain mahogany 15,828 ha (19.7%), sagebrush–herb 41,490 ha (51.8%), and snowbrush 2,140 ha (2.7%) of the 80,159 ha of summer range communities available to elk (Appendix 1). In addition, another possible nutritional carrying capacity estimate could be based on an adjustment for the smaller area within the sagebrush–herb complex used most by elk (see below). The adjusted area encompasses 70,301 ha, which includes all sagebrush–herb areas within 90 m of forested communities.

Distance of Elk in Sagebrush–Herb Communities to Woody Cover

Methods.—Several micro- and macrohabitat variables were recorded at locations of cow elk groups relocated from ground following NDOW flight searches for radio-marked elk in summers 1998–2000. Radio-telemetry relocations and general observations of cow elk groups were included in locational analyses. Elk locations were categorized as those located from late May until 9 July (spring) or from 10 July through mid-September (summer). Mid-September marked the beginning of antlerless elk hunting seasons when habitat selection changed dramatically in response to hunting pressure. Focal animal sampling was used to randomly select individual elk from groups on ground (Altmann 1974) to determine locations for habitat analyses. Two locations were selected when elk groups were distributed between

2 community types. A crude map was sketched for each elk group location to guide field workers back to exact elk group locations to conduct sampling.

Field workers recorded dominant cover type at each elk location. The distance (m) from center of elk group locations to woody cover was recorded at those locations where elk groups were using sagebrush–herb communities. I analyzed these data to provide an understanding as to the average distance elk groups diurnally foraged from forested cover.

Statistical Analyses.—My experimental design was completely randomized with time period as the main effect in the model. Distances to woody cover were grouped according to time period and were log10 transformed to meet assumptions of normality and equal variance prior to statistical testing (Oehlert 2000). Two distances were considered outliers and removed because of their influence on equal variance as assessed with a residual × predicted plot. Removing these outliers did not change statistical significance of the Type III global *F*-test. I used 1-way ANOVA (PROC GLM, SAS Institute 2001) to evaluate differences between time periods. I conducted post hoc multiple comparisons with the Tukey-Kramer HSD test to assess pairwise differences in distance of locations in sagebrush–herb communities to forested communities between time periods. Distances to woody cover from sagebrush–herb community locations are reported as raw estimates ± SE (PROC MEANS, SAS Institute 2001). Statistical significance was set at $\alpha = 0.05$. Histograms provide a graphical display of distance data for each time period.

Results.—The global ANOVA indicated a difference in distances among the time periods ($F_{5,64} = 2.76$, $P = 0.026$). Tukey-Kramer HSD tests indicated mean distances from woody cover in spring 1998 (185.3 ± 465 m) were greater than those in spring 2000 (30.5 ± 10 m); otherwise, all other comparisons did not differ (Table 5; Figs. 2, 3). All data pooled resulted in 86.0 ± 12.0 m ($n = 70$) and distances for 5 of the 6 time periods were <90 m. We thus selected 90 m around woody cover as a reasonable distance representing the sagebrush–herb area most used by elk for foraging. This area was 31,623 ha, or 39.5% of the summer range and 76.2% of the 41,490 ha sagebrush–herb cover available on summer range.

IV. ANIMAL REQUIREMENTS

A growing body of evidence suggests elk population productivity is closely aligned with nutritional conditions available to cow elk on summer–autumn ranges (Cook et al. 2001, Cook et al. in Press). Consequently, we selected a 236-kg cow elk with calf at side lactating through mid-autumn and with average dry matter intake (DMI), activity, and metabolic demands as my model animal (Cook 2002). Elk nutritional requirement calculations have typically considered 236 kg to be an average size for elk cows (Nelson and Leege 1982, Cook 2002).

Nutritional parameters incorporated in my carrying capacity model were: (1) DMI for lactating 236-kg cow elk in mid-autumn estimated at 6.9 kg/day (Cook et al., In Press) and (2) DE content (kcal/kg) required to provide maintenance performance (2,550) and optimal performance (2,750) for lactating 236-kg cow elk in early fall (Cook et al. In Press); the product of these parameters yields an average requirement of 17,595 and 18,975 kcal/day, respectively. Standing digestible energy (SDE; kcal/ha), the currency of my model was approximated as the product of DE (kcal/kg) and standing crop (kg/ha). Early fall SDE in key forages was estimated in aspen, conifer, mahogany, sagebrush–herb, and snowbrush communities. Standing crop estimates represented residual forage available, following livestock grazing. Key forages were identified in elk feeding sites and through microhistological fecal analysis (Chapter 2).

V. DELINEATION OF AUTUMN

Methods

Forage quality in aspen, curlleaf mountain mahogany (*Cercocarpus ledifolius*), and snowbrush communities was largely sufficient to meet animal demands in early August, but waned by late September (see Chapter 4). I accordingly delineated the autumn period based on limited forage quality beginning 1 September and extending to the end of the first biweekly period in November. Average temperatures by the second biweek of November tend to be below the freezing point (0 ºC), thus ending plant growth (Figs. 4A, B). In addition, elk diets predictably change this time of year as elk move to winter ranges, calves are weaned, and forage nutrient requirements change. The period from 1 September to the end of the first biweek in November yields 76 potential days of limited autumn forage quality. Autumn lengths were reduced downward from 76 days in the first instance of a biweekly accumulation of 25.4 mm of precipitation. Minimum length of autumn was bounded at 45 days. This precipitation level was set to arbitrarily represent sufficient moisture to induce fall green up of herbs, thus alleviating elk from poor foraging conditions during dry autumns. Fall rains improve forage quality in the Great Basin in years in which growing seasons begin with less than average moisture (Ganskopp and Bohnert 2001). Days of autumn based on precipitation at Pole Creek and Draw Creek SNOTEL sites were averaged each year to calculate yearly length of autumn and represent climatic variation relative to summer range latitude and elevation.

Results

Climatic data indicated autumn 1999 was 53 days and autumn 2000 was approximated to be 76 days. June through November cumulative precipitation was 2.6-times higher at the Draw Creek SNOTEL site and 2.3-times higher at the Pole Creek SNOTEL site in 1999 than in 2000. Overall, biweekly mean cumulative precipitation was lower and biweekly mean temperatures higher in 2000 than in 1999 (Figs. 4A, B).

LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Bechtold. J.P. 1996. Chemical characterization of natural mineral springs in northern British Columbia, Canada. Wildlife Society Bulletin 24:649–654.

Beck, J. L., J. T. Flinders, D. R. Nelson, C. L. Clyde, H. D. Smith, and P. J. Hardin. 1996. Elk and domestic sheep interactions in a north-central Utah aspen ecosystem. U.S. Forest Service Research Paper INT-RP-491.

Bishop, Y. M. M., S. E. Fienberg, and D. W. Holland. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, Massachusetts, USA.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, New York, New York, USA.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and inference: a practical information–theoretic approach. Springer-Verlag, New York, New York, USA.

Cook, J.G. 1990. Habitat, nutrition, and population ecology of two transplanted bighorn sheep populations in southcentral Wyoming. Ph.D. Thesis, University of Wyoming, Laramie, Wyoming, USA.

_____. 2002. Nutrition and food habits. Pages 259–349 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Second edition. Smithsonian Institution Press, Washington, D.C.

_____, B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. In press. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monograph.

Cook, R.C., D.L. Murray, J.G. Cook, P. Zager, and S.L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology 79:845–853.

DeYoung, R. W., E. C. Hellgren, T. E. Fulbright, W. R. Robbins, Jr., and I. D. Humphreys. 2000. Modeling nutritional carrying capacity for translocated desert bighorn sheep in western Texas. Restoration Ecology 8:57–65.

Fowler, J., L. Cohen, and P. Jarvis. 1998. Practical statistics for field biology. Second edition. John Wiley and Sons, Limited. Chichester, West Sussex, England.

Ganskopp, D. and D. Bohnert. 2001. Nutritional dynamics of 7 northern Great Basin grasses. Journal of Range Management 54:640–647.

Goodman, L. A. 1960. On the exact variance of products. Journal of the American Statistical Association 55:708–713.

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.

_____, and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551–560.

_____, and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.

Holechek, J. L. 1988. An approach for setting the stocking rate. Rangelands 10:10–14.

_____, R. D. Pieper, and C. H. Herbel. 1989. Range management: principles and practices. Regents/Prentice Hall, Engelwood Cliffs, New Jersey, USA.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Interagency Technical Reference. 1996. Sampling vegetation attributes. U.S. Forest Service; U.S. Natural Resource Conservation Service: Grazing Land Technology Institute; and, U.S. Bureau of Land Management. U.S. Bureau of Land Management, National Applied Resource Sciences Center, BLM/ST-96/002+1730.

Irwin, L. L., and J. M. Peek. 1983. Elk, *Cervus elaphus*, foraging related to forest management and succession in Idaho. Canadian Field-Naturalist 97:443–447.

Jensen, M. E., L. S. Peck, and M. V. Wilson. 1988. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. Great Basin Naturalist 48:403–421.

Kincaid, R. 1988. Macro elements for ruminants. Pages 326–341 *in* D.C. Church, editor. The ruminant animal: digestive physiology and nutrition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Mautz, W. W. 1978. Nutrition and carrying capacity. Pages 321–348 *in* J. L. Schmidt and D. L. Gilbert, editors. Big game of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

McCall, T. C., R. D. Brown, and L. C. Bender. 1997. Comparison of techniques for determining nutritional carrying capacity of white-tailed deer. Journal of Range Management 50:33–38.

Nelson, J. R. and T. A. Leege. 1982. Nutritional requirements and food habits. Pages 323–367 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Oehlert, G. W. 2000. A first course in the design and analysis of experiments. W. H. Freeman and Company, New York, New York, USA.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.

SAS Institute. 2001. SAS/STAT User's Guide, Release 8.2. SAS Institute, Incorporated, Cary, North Carolina, USA.

U.S. Forest Service. 1988. Soil and vegetation communities of the Pole Creek bench area. U.S. Forest Service, Humboldt National Forest, Elko, Nevada.

Vallentine, J. F. 1990. Grazing management. Academic Press, San Diego, California, USA.

Table 1. Seasonal herbaceous standing crop (kg DM/ha; lsmeans ± SE) in aspen and mahogany communities, Jarbidge Mountains, Nevada, 1999 and 2000.

Community	Annual forbs	Perennial forbs	Perennial graminoids
Aspen 1999			
Early summer	126.1 ± 22.1^{AB}	594.5 ± 111.1^{A}	201.1 ± 57.2^{AB}
Mid-summer	58.4 ± 15.2^{C}	202.5 ± 65.0^{BDE}	433.3 ± 122.2^{A}
Early fall	2.2 ± 2.4^{D}	94.8 ± 44.5^{BDE}	143.3 ± 40.7^{AC}
Aspen 2000			
Early summer	172.0 ± 19.6^{A}	498.0 ± 91.2^{AC}	199.6 ± 49.0^{AC}
Mid-summer	51.2 ± 10.7^{BC}	158.9 ± 51.5^{BDE}	170.4 ± 41.8^{AC}
Early fall	9.8 ± 4.7^{D}	124.2 ± 45.5^{BDE}	111.4 ± 27.3^{BC}
Mahogany 1999			
Early summer	24.9 ± 9.1^{CD}	208.0 ± 65.7^{BCE}	113.8 ± 32.4^{BC}
Mid-summer	3.5 ± 3.6^{D}	50.3 ± 32.4^{DF}	105.6 ± 29.8^{BC}
Early fall	2.6 ± 2.9^{D}	42.6 ± 29.8^{DF}	102.7 ± 29.1^{BC}
Mahogany 2000			
Early summer	13.8 ± 5.7^{CD}	202.4 ± 58.1^{E}	138.4 ± 34.0^{AC}
Mid-summer	8.2 ± 4.4^{D}	102.6 ± 41.4^{EF}	146.2 ± 35.9^{AC}
Early fall	4.5 ± 3.2^{D}	81.5 ± 36.9^{EF}	99.7 ± 24.5^{BC}

^{ABCDEF}Estimates in the same column followed by the same superscript are not different ($P > 0.05$) as tested by Tukey-Kramer HSD tests.

Table 2. Current annual growth standing crop (kg DM/ha; lsmeans ± SE) for dominant browse species in aspen, curlleaf mountain mahogany, and snowbrush communities, Jarbidge Mountains, Nevada, 1999 and 2000.

Species by community	1999			2000		
	Early summer	Mid-summer	Early fall	Early summer	Mid-summer	Early fall
Aspen						
Aspen	5.7 ± 5.2^{AB}	38.7 ± 13.5^{AC}	3.1 ± 3.8^{B}	12.7 ± 6.4^{ABC}	38.5 ± 11.1^{C}	13.1 ± 6.5^{ABC}
Snowberry	15.7 ± 15.5^{A}	7.5 ± 11.1^{A}	6.2 ± 9.7^{A}	13.7 ± 14.0^{A}	12.4 ± 13.4^{A}	9.5 ± 11.7^{A}
Mahogany						
Mahogany	14.0 ± 7.0^{A}	23.0 ± 11.6^{AB}	14.1 ± 7.0^{A}	38.4 ± 17.8^{AB}	42.3 ± 19.6^{AB}	63.7 ± 29.4^{B}
Snowberry	10.9 ± 12.1^{AD}	34.6 ± 16.5^{ABD}	34.8 ± 19.6^{ABCD}	75.4 ± 31.0^{BCE}	57.8 ± 21.3^{C}	26.8 ± 14.9^{DE}
Snowbrush						
Snowbrush	N/A	N/A	1,819.2 ± 405.3^{A}	1,845.1 ± 90.9^{A}	1,829.3 ± 267.6^{A}	1,662.6 ± 120.7^{A}

^{ABCDE}Estimates in the same row followed by the same superscript are not different ($P > 0.05$) as tested by Tukey-Kramer HSD tests.

Table 3. Forage available (kg/ha) in early fall in sagebrush–herb communities, Jarbidge Mountains, Nevada. Data from Tables 2, 4, and 6 in Jensen al. (1988)[a] represent 8 sagebrush–herb community types in the study area. Original data were reduced to reflect allowable U.S. Forest Service use levels[b] to represent annual livestock consumption. Snowberry represents consumable woody browse.

Sagebrush community type	Forage available (kg/ha)		
	Forbs	Graminoids	Snowberry
Artemisia arbuscula / *Festuca idahoensis*	38.0	169.2	6.3
A. a. / *Festuca idahoensis* / *Poa secunda*	32.4	99.2	5.0
A. a. / *Pseudoroegneria spicata*	29.2	53.2	2.8
A. vaseyna / *Elymus cinereus*	260.0	104.0	0.0
A. v. / Festuca idahoensis	73.2	137.2	7.8
A. v. / *Pseudoroegneria spicata*	54.0	62.4	10.9
A. v. / *Symphoricarpos oreophilus* / *Bromus marginatus*	214.4	89.6	51.1
A. v. / *Symphoricarpos oreophilus* / *Pseudoroegneria spicata*	112.0	74.8	42.0
Mean	101.7	98.7	15.7
SE	31.4	13.7	6.9

[a] Jensen, M.E., L.S. Peck, and M.V. Wilson. 1988. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. Great Basin Naturalist 48:403–421.

[b] Humboldt-Toiyabe National Forest allowable use levels in non-riparian rangeland of 60% for herbs and 50% for current annual growth of shrubs in deferred rotation allotments.

Table 4. Forage available (kg/ha) in early fall in conifer communities, Jarbidge Mountains, Nevada. Data from 3 subalpine fir communities on the Pole Creek Bench in the northern portion of the study area (U.S. Forest Service 1988)[a]. Original data were reduced to reflect allowable U.S. Forest Service use levels[b] to represent annual livestock consumption. Snowberry represents consumable woody browse.

Forage category	Forage available (kg/ha)	
	Mean	SE
Forbs	31.9	29.1
Grasses	24.2	7.4
Snowberry	1.1	0.0

[a] U.S. Forest Service. 1988. Soil and vegetation communities of the Pole Creek Bench area. U.S. Forest Service, Humboldt National Forest, Elko, Nevada, USA.

[b] Humboldt-Toiyabe National Forest allowable use levels in non-riparian rangeland of 60% for herbs and 50% for current annual growth of shrubs in deferred rotation allotments.

Table 5. Distances (m) of cow elk group locations in sagebrush–herb communities to woody cover in spring (late-May–10 Jul) and summer (10 Jul–mid-Sep), Jarbidge Mountains, Nevada, 1998–2000.

Time period	*n*	Mean	SE
1998			
Spring	12	185.3^{A}	46.5
Summer	22	77.1^{AB}	15.1
1999			
Spring	4	38.3^{AB}	15.0
Summer	11	55.8^{AB}	12.4
2000			
Spring	7	30.5^{B}	10.0
Summer	14	79.9^{AB}	26.2

^{AB}Means in the same column followed by the same uppercase superscript are not different ($P > 0.05$) as tested by Tukey-Kramer HSD tests.

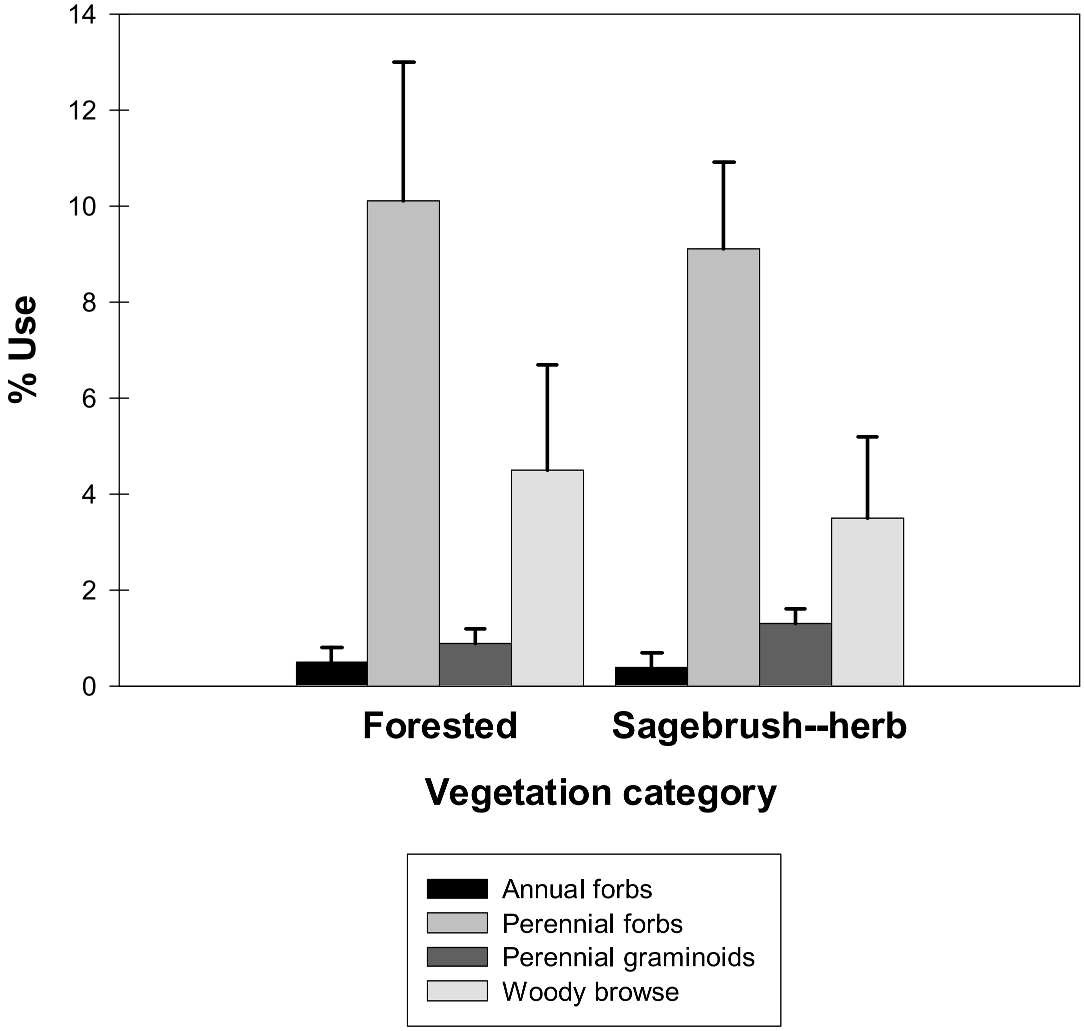


Fig. 1. Mean percent use (+ SE) of annual forbs, woody browse, perennial forbs, and perennial graminoids at 37 elk feeding sites, Jarbidge Mountains, Nevada, 1999 and 2000. Aspen and mahogany feeding sites were combined into a forested category and feeding sites in sagebrush and meadows were combined into a sagebrush–herb category. Data were pooled because there were no differences among years or spring and summer seasons as tested with 1-way ANOVA. Forested and sagebrush–herb use estimates within forage categories also did not differ, but are presented separately.

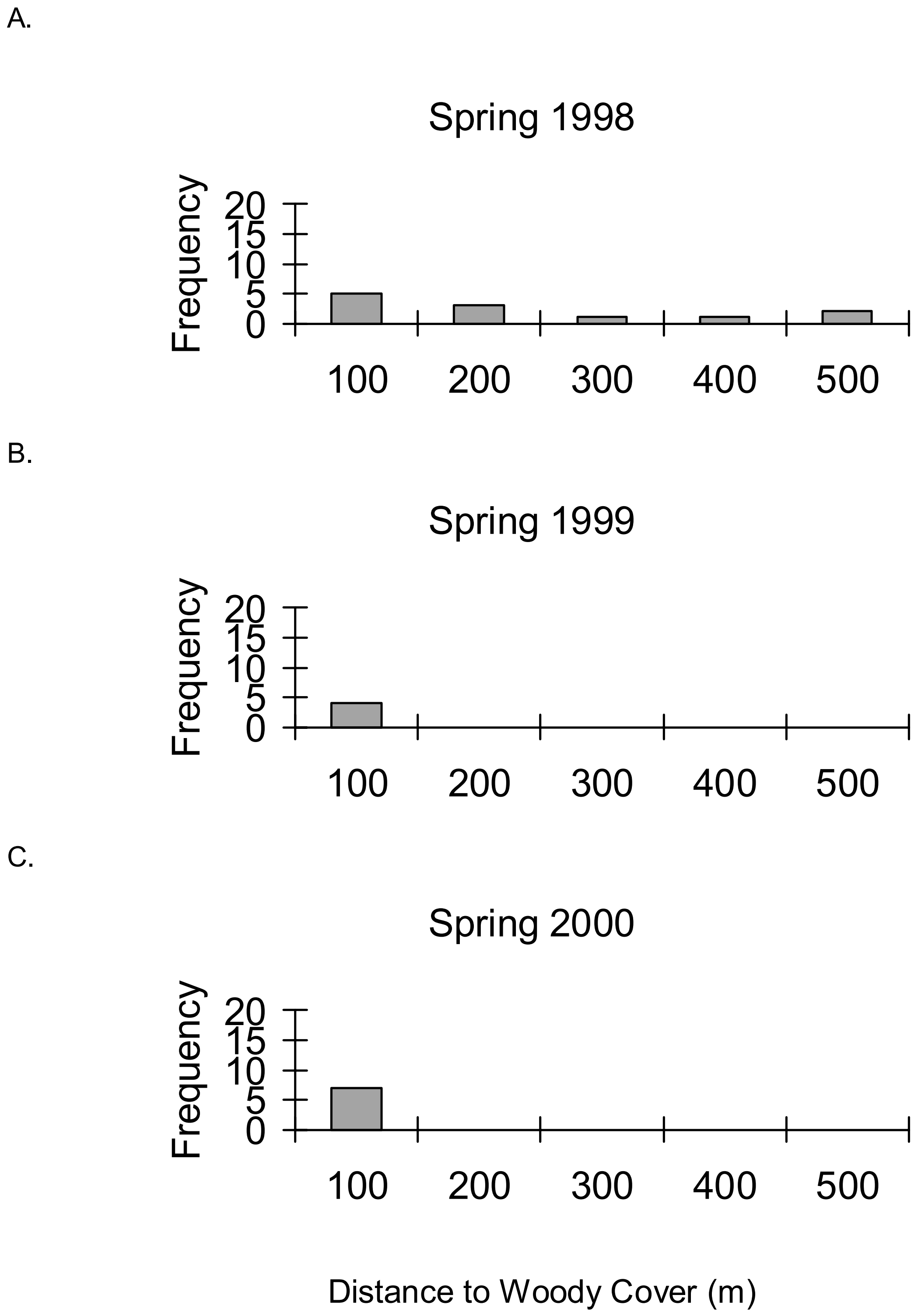


Fig. 2. Histograms of distances (m) of cow elk group locations in sagebrush–herb communities to woody cover in spring (late-May–10 Jul). A, spring 1998 (*n* = 12). B, spring 1999 (*n* = 4). C, spring 2000 (*n* = 7).

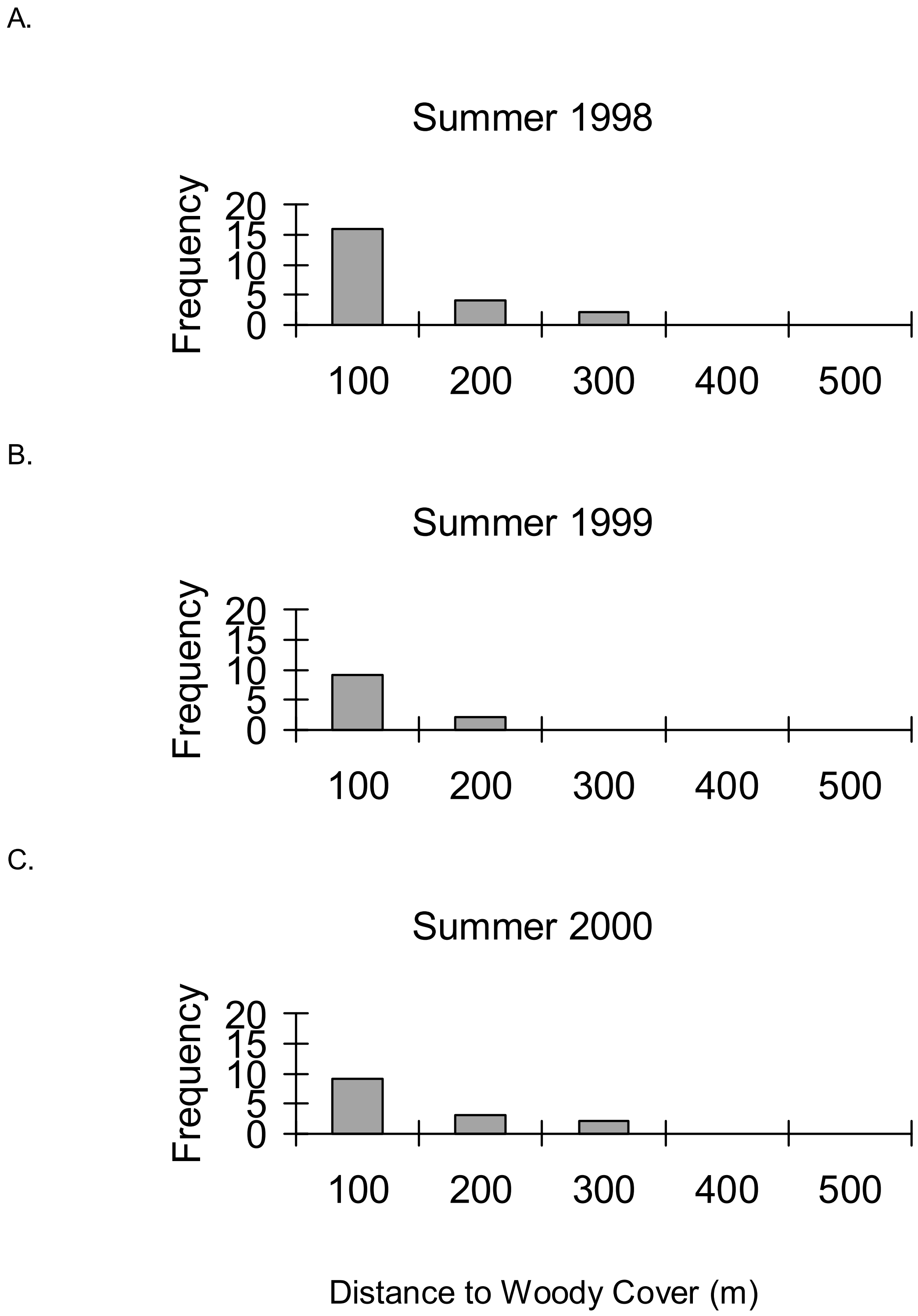
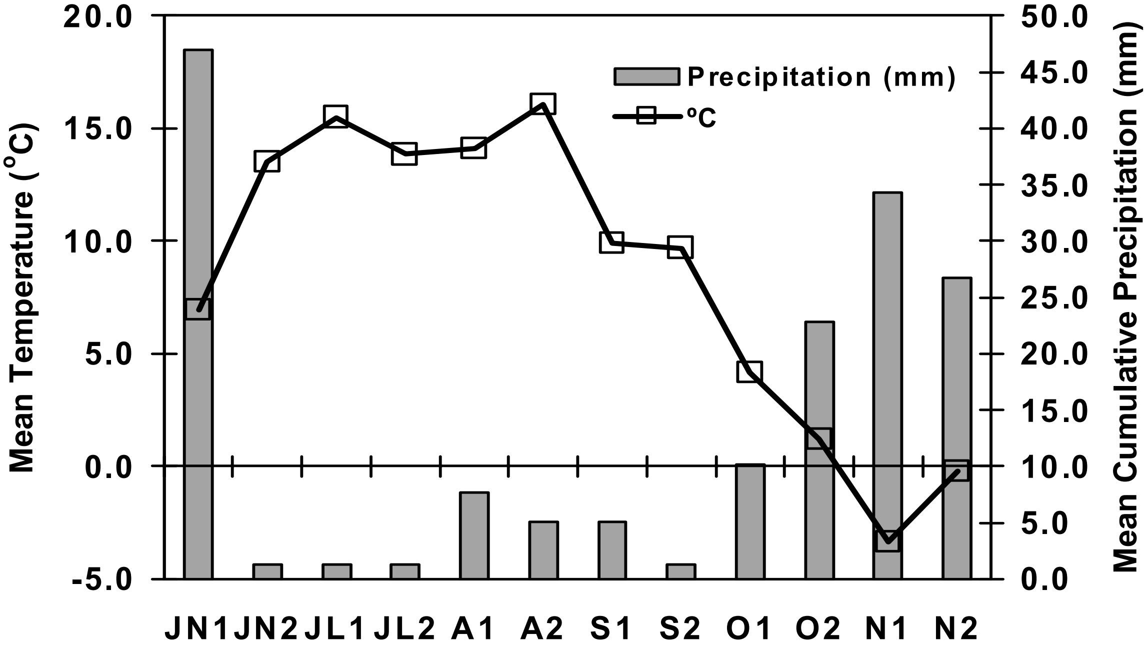


Fig. 3. Histograms of distances (m) of cow elk group locations in sagebrush–herb communities to woody cover in summer (10 Jul–mid-Sep). A, summer 1998 (*n* = 22). B, summer 1999 (*n* = 11). C, summer 2000 (*n* = 14).

A. 1999 climograph



B. 2000 climograph

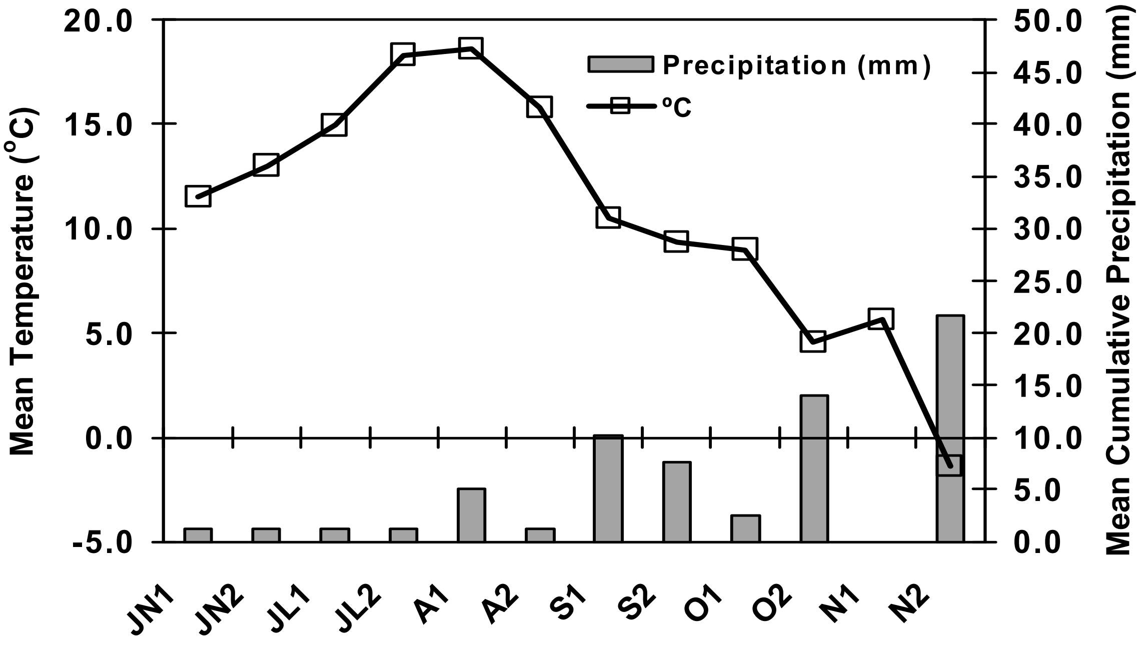


Fig. 4. Climograph of mean biweekly temperature (ºC) and cumulative precipitation (mm), Jarbidge Mountains, Nevada, Jun–Nov 1999 (A) and 2000 (B). Data are averages from each 2-week period within months from the Draw Creek (2,300 m) and Pole Creek (2,540 m) Natural Resource Conservation Service SNOTEL Sites.