

GREAT BASIN SUMMER RANGE FORAGE QUALITY: DO PLANT NUTRIENTS MEET ELK REQUIREMENTS?

Jeffrey L. Beck^{1,2} and James M. Peek¹

ABSTRACT.—Understanding the relative ability of forages to meet the needs of prime-age females, the productive component of elk (*Cervus elaphus*) populations, is necessary to decipher reasons for declines and potential for population growth. Information on forage nutrient dynamics for elk on Great Basin summer–fall ranges is lacking. Our primary objectives were to estimate nutrient levels in common elk forage species in northeastern Nevada at 3 time periods and evaluate whether nutrient levels met good requirements for lactating cow elk at time periods across summers. We compared crude protein, digestible energy, and macromineral levels in 2 forbs, 6 grasses, and 4 woody browse forage species to requirements for lactating cow elk in early summer, midsummer, and early fall 1999 and 2000. Spurred lupine (*Lupinus caudatus*) and snowbrush ceanothus (*Ceanothus velutinus*) were the most proteinaceous plants, exceeding requirements across all seasons. By midsummer, protein levels in all grasses were below elk requirements (12%). Digestible energy was the most limiting nutrient with woody browse meeting lactating cow elk requirements only in early fall (2750 kcal · kg⁻¹). Sodium levels never exceeded about 10% of the required 600 µg · g⁻¹. The potential for maintaining a relatively high density of elk at forage-quality levels that fulfill requirements declines as summers progress on Great Basin summer ranges. Maintaining highly productive elk herds in the Great Basin requires that managers maintain plant communities with a diversity of forbs, grasses, and browse to provide for nutritional needs of lactating cows and their growing calves.

Key words: female elk summer nutritional ecology, *Cervus elaphus*, crude protein, digestible energy, macrominerals, Great Basin, Nevada.

Elk (*Cervus elaphus*) winter survival can depend on endogenous energy reserves anabolized during summer and fall and thus depends on forage quality and quantity available on summer ranges (Mautz 1978, Baker and Hobbs 1982). Recent work suggests that elk populations with reduced pregnancy rates for prime-age females with calves are probably indicative of summer–fall ranges with inadequate nutrient supplies (Cook et al. 2001). Moreover, high elk pregnancy rates do not necessarily reflect adequate nutritional conditions. Despite high pregnancy rates, adult females on nutritionally marginal summer–fall ranges may delay breeding and parturition; growth of calves and yearlings may be reduced and yearling breeding may be lowered (Cook et al. 2004). Energetic needs of lactating cow elk in summer are 2 or 3 times higher than during gestation (Robbins 1993); thus, foraging options at that time have implications for elk population productivity (Wisdom and Cook 2000).

Archaeological excavations in Oregon and Nevada indicate elk were present post-Pleis-

tocene in the Great Basin (Nevada Division of Wildlife 1997); however, historical densities and distributions are unknown. Elk were rare in Nevada following white settlement (Hall 1946, Murie 1951, O’Gara and Dundas 2002) until translocation efforts began in the 1930s. By 1998 over 5000 elk existed among several populations in central and eastern Nevada (Nevada Division of Wildlife 1997, O’Gara and Dundas 2002). Phosphorus, energy, and protein are 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 Great Basin 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

¹Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1136.

²Present address: Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166.

decipher reasons for declines and potential for population growth (Alldredge et al. 2002).

We conducted a nutritional assessment for elk inhabiting Great Basin mountain summer range where the growth of important foraging communities such as aspen (*Populus tremuloides*) is greatly restricted by temperature and moisture compared to more mesic regions (Mueggler 1988). We estimated nutritional content of 12 common elk forages in the Great Basin across 3 time periods in 2 summers and compared these estimates with requirements for a lactating cow elk. Our specific objectives were to (1) estimate seasonal crude protein (CP), digestible energy (DE), and macromineral levels in common summer forage species; (2) evaluate whether forage plant nutrient levels met seasonal lactating cow elk requirements for good performance across summers; and (3) identify management implications in relation to elk population growth.

We selected a cow elk nursing a calf through mid-fall and with average dry matter intake, activity, and metabolic demands as our model to compare CP, DE, and macromineral requirements in summer (Alldredge et al. 2002, Cook 2002). Because we address requirements for plant nutrients and not animal nutrient intake, our comparisons apply to lactating cow elk of all body weights. We evaluated forage quality in relation to requirements for good performance in lactating cow elk. Good requirements are levels where cows with calves are assured to experience no, or virtually no, limitations in reproduction, survival, or growth from nutrition (Cook et al. 2004). In comparison, requirements for maintenance are nutritional levels required to maintain endogenous nutrient levels, particularly body fat levels, of adult cows with calves at heel. At maintenance, nutritional deficiencies do not yet affect elk performance, but when animals encounter nutrient levels below maintenance they will show reduced body condition and reproduction due to limited nutrients. In addition, maintenance requirements will likely only support low to moderate calf growth (Cook et al. 2004).

STUDY AREA

Our study area comprised Nevada Division of Wildlife Hunt Unit 072 (41°30' to 42°00'N and 115°00' to 115°30'W) in northeastern Nevada. Hunt Unit 072 consists of 1665 km²

ranging in elevation from 1633 m to 3287 m. We delineated all areas ≥ 2135 m as elk summer range because 93% of collared cow elk located on radiotelemetry flights across summers 1998–2001 were found in this elevational zone (Beck 2003). Summer range included 48%, or 802 km², of the study area and was administered by Forest Service (92%), Bureau of Land Management (5%), and private interests (3%). In the study area northern slopes drain into the Snake River, while southern slopes drain into the Great Basin (USDA Forest Service 1981).

Snowpack provides most moisture for spring forage production. Snow water equivalents on 1 April at 2 Natural Resource Conservation Service SNOTEL sites, Draw Creek (2300 m) in the south and Pole Creek Ranger Station (2540 m) in the north, were 88% and 104%, and 91% and 90%, of 30-year (1971–2000) averages (Draw Creek, 297 mm; Pole Creek, 523 mm) in 1999 and 2000, respectively. Mean monthly temperatures (°C) averaged from June through October were 11 in 1999 and 14 in 2000 at Draw Creek (1991–2000, \bar{x} = 12), and 10 in 1999 and 11 in 2000 at Pole Creek (1991–2000, \bar{x} = 10). June through October 1999 and 2000 cumulative precipitation (mm) was 104 and 41 at Draw Creek (1985–2000, \bar{x} = 100) and 101 and 51 at Pole Creek Ranger Station (1985–2000, \bar{x} = 138).

Dominant summer range communities were a sagebrush-herb complex composed of mountain big sagebrush (*Artemisia tridentata vaseyana*) and little sagebrush (*A. arbuscula*) interspersed with herbaceous meadows, aspen, curl-leaf 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. Sagebrush-herb communities covered 52% of the study area followed by curl-leaf mountain mahogany (20%), aspen (15%), conifer (11%), and snowbrush ceanothus (2%). Lewis (1975) provided detailed lists of herbaceous species in each community. Telemetry work indicated elk used curl-leaf mountain mahogany communities most frequently in late spring and early summer. Elk foraged in aspen, sagebrush-herb, and snowbrush ceanothus communities extensively in summer and early fall. Conifer communities typically lacked substantial herb and shrub layers and were used primarily for cover on summer range.

We collected forage samples in 1999 and 2000 from the Black Spring, Spring Creek, and Wilson Creek cow/calf grazing allotments. Black Spring was managed with Caudle Creek allotment (53 km²) as a deferred rotation grazing system with a stocking rate of 82 animal unit months (AUM) · km⁻² from 6 July through 11 October 1999 and 72 AUM · km⁻² from 1 July through 16 September 2000. Spring Creek allotment (31 km²) was managed under a 3-pasture rest rotation grazing system with a stocking rate of approximately 140 AUM · km⁻² from 1 July through 15 October 1999 and 2000. Wilson Creek allotment (24 km²) was managed under a 3-pasture deferred rotation grazing system with a stocking rate of 70 AUM · km⁻² from 1 July through 30 September 1999 and 66 AUM · km⁻² from 7 July through 30 September 2000.

Elk were reintroduced into the Jarbidge Mountains during 1990–1995 (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 to 2000 (Beck 2003). Elk share summer range with mule deer, pronghorn (*Antilocapra americana*), cattle, and domestic sheep. Ratios of calves per 100 cows from 1 July to mid-September 1998–2000 averaged 52 (range = 32–57; Beck 2003), 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 1.15 following release from hunting (2000–2003), indicative of population growth under current conditions (Beck 2003). New management objectives call for elk to increase to 1000 ± 100 by 2010, at which time objectives will be reevaluated (Nevada Division of Wildlife 2000).

METHODS

Forage Collections

We evaluated 2 forbs, 6 grasses, and 4 woody species commonly used by elk for food in our study area (Table 1). These forage plants collectively formed 45%–64% of spring and 53%–64% of summer 1998–2000 elk diets determined through microhistological fecal analysis (Beck and Peek 2005). We encourage readers to consult Beck and Peek (2005) for methods we used to evaluate diet composition

and to fully evaluate the results. These species and/or genera inhabit a variety of important plant communities common to mountain summer range across the Great Basin (Table 1). Forbs collected were arrowleaf balsamroot (*Balsamorhiza sagittata*) and spurred lupine (*Lupinus caudatus*). Grasses included blue-bunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), Kentucky bluegrass (*Poa pratensis*), mountain brome (*Bromus marginatus*), Sandberg bluegrass (*P. secunda*), and needlegrasses (*Achnatherum* spp.), primarily Columbia needlegrass (*A. nelsonii*) and Letterman's needlegrass (*A. lettermanii*). Woody browse included aspen, curl-leaf mountain mahogany, mountain snowberry (*Symphoricarpos oreophilus*), and snowbrush ceanothus (Table 1).

We collected forage samples from the Black Spring, Spring Creek, and Wilson Creek cow/calf grazing allotments during early summer (late June), midsummer (early August), and early fall (late September) 1999 and 2000. We initiated forage collections in each allotment within the same 2-week period in each of the 3 months over both years. We collected plant tissue samples from the same predetermined locations at each time period in each grazing allotment to incorporate forage quality influenced by landscape variability in plant communities and to provide comparable results across time periods. Forage sampling locations were typically adjacent to vegetation plots that we sampled to provide estimates of seasonal standing crop (Beck 2003). We typically collected individual plant species from communities where they were most abundant in the study area (e.g., Idaho fescue, Sandberg bluegrass, and spurred lupine were collected in sagebrush-herb communities). As summers progressed, we often found it necessary to increase our search area to find ungrazed plants to collect samples from.

We clipped ungrazed plants to mimic portions of plants eaten by elk at thirty-seven 0.01-ha feeding sites (Beck 2003); these typically included the inflorescence and basal leaves in forbs and grasses, and succulent shoots and current annual growth in shrubs. We ensured that elk solely used feeding sites by returning within 1 week of observing feeding elk and then searching each site for tracks and/or feces from other ungulates; consequently, we did not examine elk feeding sites used by

TABLE 1. Common forage plant species evaluated in nutritional analyses, communities inhabited by these plants, and spring and summer elk diet composition for these forage species, Jarbidge Mountains, Nevada, 1999 and 2000. Diet data from Table 1 in Beck and Peek (2005).

Species	Community ^a	Elk diets (%)			
		1999		2000	
		Spring ^b	Summer ^c	Spring	Summer
GRASSES					
Bluebunch wheatgrass	M, SH	8	5	2	5
Idaho fescue	SH	2	7	1	5
Kentucky bluegrass	A, SH	0	0	3	6
Mountain brome	A, SH	7	1	2	3
Sandberg bluegrass	SH	7	6	0	0
Needlegrasses	A, M, SH	2	3	2	6
FORBS					
Arrowleaf balsamroot	M, SH	<1	1	7	<1
Spurred lupine ^d	A, M, SH	6	29	17	38
WOODY BROWSE					
Aspen	A	0	0	0	0
Curl-leaf mountain mahogany	M	7	0	5	0
Mountain snowberry	A, C, M, SH, SC	2	0	0	0
Snowbrush ceanothus	SC	22	4	6	0

^aPlant communities inhabited by forage plants are A = aspen; C = conifer; M = curl-leaf mountain mahogany; SH = sagebrush-herb; and SC = snowbrush ceanothus.

^bSpring fecal collections included feces from adult elk in cow elk groups and mixed groups of cow and bull elk (Beck and Peek 2005).

^cSummer fecal collections included feces only from adult elk in cow elk groups (Beck and Peek 2005).

^dLupines were not discernable to species in microhistological fecal analysis, and thus diet percentages represent all lupine species (Beck and Peek 2005).

other ungulates (Beck and Peek 2005). At each collection we clipped fresh material and removed old growth to form ≥ 30 g fresh weight samples from multiple plants to encompass variation among plants. We clipped a greater number of plants from small-stature plants such as Sandberg bluegrass and Idaho fescue. We air-dried samples in paper bags to prevent fungal growth and later dried samples in a forced-air oven at 60°C. We ground oven-dried samples to 2 mm (Svejcar and Vavra 1985) and stored them 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 Analytical Sciences Laboratory at the University of Idaho conducted organic and macromineral compositional analyses. Total nitrogen (N) and sulfur (S) were determined following McGeehan and Naylor's (1988) combustion technique. Concentrations ($\mu\text{g} \cdot \text{g}^{-1}$) of calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P), and sodium (Na) were determined by inductively coupled plasma-atomic emission spectroscopy (Anderson 1996). Percent crude protein was approximated as $6.25 \times$

[%N] (Robbins 1993). We report only 1999 Na values above detectable levels because all samples were below detectable Na levels in 2000.

We estimated apparent IVDMDs using techniques described by Pearson (1970) and Tilley and Terry (1963). We collected rumen in-oculum from fistulated beef cows maintained on a diet of approximately 1/3 alfalfa (*Medicago sativa*) and 2/3 grass hays. We fed cattle this diet to mimic the forage-based diet of elk in the Jarbidge Mountains and to produce a rumen microflora similar to that for elk on the same diet. We used Dacron[®] filter bags with 95% of pores <30 microns (Ankom Technology, Macedon, NY, USA) to contain material during fermentation. Triplicates of each sample were digested for 48 hours to obtain mean percentage IVDMD with CV $\leq 5\%$. We conducted additional replications until at least 2 replicates could be averaged with an accompanying CV $\leq 5\%$. We increased June and August IVDMD estimates by 11% and 6%, respectively, to correct for underestimation related to air-drying forages that occurs at these time periods (Cook 1990). We determined GE with bomb calorimetry for duplicate composite forb, grass, and woody browse samples representing each allotment and time period; CVs for

gross energy duplicates were all $\leq 3\%$. We approximated DE ($\text{kcal} \cdot \text{kg}^{-1}$) as the product of mean apparent IVDMD for each forage 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; we selected the covariance structure with the lowest AIC value (Burnham and Anderson 2002).

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 \times season interaction were fixed effects, while allotment and the allotment \times season interaction were random effects in our model. We assessed assumptions and conducted tests for all ANOVAs with Statistical Analysis System software (SAS, PROC MIXED; SAS Institute 2001). We removed outlier observations if they had a large influence on model variance as detected in residual \times predicted plots. Removing outliers had no effect on ANOVA statistical significance. We transformed CP proportions with the arcsine square root transformation, and we used the natural log transformation of DE data to 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. We qualitatively compared ranges in minerals to gestation and early lactation requirements for beef cattle (National Research Council 1984, 1996).

There was no significant allotment \times species interaction ($P > 0.05$) for CP or DE, which justified averaging species responses over allotments. We constructed 95% confidence

intervals (CI) 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 good nutritional status for lactating cow elk in summer (Cook 2002, Cook et al. 2004). We conducted post hoc multiple comparisons with the Tukey-Kramer HSD test to separate means when significant main effects or interactions were detected. We used Spearman's rank order correlations (SAS PROC CORR; SAS Institute 2001) to examine relationships between percentages of the 12 forage plants in spring and summer elk diets (Table 1) and CP and DE levels in early summer forage (compared to spring cow and mixed group elk diets), mid-summer forage (compared to summer cow elk group diets), and early fall forage (compared to summer cow elk group diets) in 1999 and 2000. We report estimates as mean $\pm 95\%$ CI, and we set statistical significance at $\alpha = 0.05$.

RESULTS

Crude Protein

We collected 105 and 108 forage samples in 1999 and 2000, respectively. Aspen was not collected in early summer 1999. Crude protein decreased among all species across seasons (Table 2). 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 \times season interaction ($F_{22, 152} = 417.13$). Idaho fescue and Sandberg bluegrass CP levels were below good requirements for lactating cow elk in all seasons, while spurred lupine and snowbrush ceanothus CP levels exceeded good levels in all seasons (Table 2). Herbaceous CP levels generally exceeded good requirements in early summer and declined below good elk levels in midsummer and early fall. However, by midsummer, CP in all grasses was below good requirements for cow elk. Highest CP was detected in spurred lupine in early summer ($22.7 \pm 4.7\%$), and lowest was detected in bluebunch wheatgrass in early fall ($4.0 \pm 1.0\%$). Curl-leaf mountain mahogany, mountain snowberry, snowbrush ceanothus, spurred lupine, and Kentucky bluegrass all maintained levels above good requirements for lactating cow elk in early fall (Table 2). Percent of forage species in spring 2000 elk diet correlated with early summer 2000 CP levels and

TABLE 2. Summer and early fall crude protein (% DM \pm 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 were compared to good requirements for lactating cow elk with 1-tailed, 1-sample t tests.

Species	Early summer (%)	Midsummer (%)	Early fall (%)
FORBS			
Arrowleaf balsamroot	16.7 \pm 1.6 ^A	7.6 \pm 1.5 ^{B*}	5.6 \pm 1.7 ^{B*}
Spurred lupine	22.7 \pm 4.7 ^A	17.4 \pm 3.4 ^B	9.8 \pm 1.7 ^C
GRASSES			
Bluebunch wheatgrass	14.9 \pm 2.8 ^A	7.6 \pm 1.6 ^{B*}	4.0 \pm 1.0 ^{C*}
Idaho fescue	11.6 \pm 1.2 ^{aA*}	7.0 \pm 1.2 ^{B*}	5.6 \pm 1.2 ^{B*}
Kentucky bluegrass	15.4 \pm 1.7 ^A	10.4 \pm 1.1 ^{B*}	7.7 \pm 0.5 ^B
Mountain brome	19.5 \pm 5.7 ^A	10.2 \pm 1.3 ^{B*}	6.3 \pm 1.6 ^{C*}
Needlegrasses	15.3 \pm 2.9 ^A	9.9 \pm 2.6 ^{B*}	4.4 \pm 0.8 ^{C*}
Sandberg bluegrass	7.7 \pm 1.4 ^{A*}	6.7 \pm 2.0 ^{A*}	5.8 \pm 1.4 ^{A*}
WOODY BROWSE			
Aspen	13.4 \pm 3.2 ^{bA}	12.2 \pm 1.1 ^A	5.9 \pm 1.1 ^{B*}
Curl-leaf mountain mahogany	13.1 \pm 3.6 ^A	9.6 \pm 0.7 ^{A*}	9.0 \pm 1.1 ^A
Mountain snowberry	14.9 \pm 3.2 ^A	9.4 \pm 1.6 ^{B*}	6.7 \pm 1.8 ^B
Snowbrush ceanothus	17.0 \pm 3.4 ^A	12.7 \pm 0.3 ^B	9.7 \pm 0.5 ^B
GOOD REQUIREMENTS^c	14	12	8

^aOutlier removed ($n = 5$).

^bJune 2000 aspen only ($n = 3$).

^cGood requirements are levels where cows with calves are assured to experience no, or virtually no, limitations in reproduction, survival, or growth from nutrition (Cook et al. 2004). Crude protein good requirements are 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 good requirement ($P < 0.05$) as tested by 1-tailed, 1-sample t test.

was the only significant diet and CP correlation ($r_s = 0.77$, $n = 12$, $P = 0.004$).

Digestible Energy

Digestible energy in all forbs and grasses declined from early summer to early fall (Table 3). 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 \times season interaction ($F_{22, 149} = 8.77$). Sandberg bluegrass was the only species with DE below good requirements in all seasons. Three woody browse species, but not curl-leaf mountain mahogany in midsummer, maintained DE levels above lactating cow elk good requirements from early summer through early fall (Table 3). Arrowleaf balsamroot, spurred lupine, and mountain brome DE levels satisfied cow elk good requirements in midsummer, but no herbaceous forage met 2750 kcal \cdot kg⁻¹ DE good requirements in early fall (Table 3). There were no significant correlations between percentages of forage species in 1999 and 2000 elk diets and DE.

Macrominerals

Mineral concentrations varied widely among species, with no predictable patterns detected among allotments, species, seasons, or years. Sodium levels in all forages were below re-

quirements during all time periods. Highest Na level was 62 $\mu\text{g} \cdot \text{g}^{-1}$, well below the 600 $\mu\text{g} \cdot \text{g}^{-1}$ minimum Na requirement (Table 4). Ranges in S in Sandberg bluegrass and curl-leaf mountain mahogany were also below requirements; however, upper mean ranges in Sandberg bluegrass (1467 $\mu\text{g} \cdot \text{g}^{-1}$) and curl-leaf mountain mahogany (1400 $\mu\text{g} \cdot \text{g}^{-1}$) approached 1500 $\mu\text{g} \cdot \text{g}^{-1}$ requirements (Table 4). Ranges in all other minerals in all other plants exceeded minimum requirements (Table 4). 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 4). 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 4).

DISCUSSION

During early growth stages, herbaceous forages typically provide adequate nutrients for growth, improvement of body condition, and milk production (Cook 1972, Vallentine 1990). Protein in forbs and grasses is typically less than or equal to shrubs, decreases more rapidly,

TABLE 3. Summer and early fall digestible energy (kcal · kg⁻¹ DM ± 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 were compared to good requirements for lactating cow elk with 1-tailed, 1-sample t tests.

Species	Early summer (kcal · kg ⁻¹)	Midsummer (kcal · kg ⁻¹)	Early fall (kcal · kg ⁻¹)
FORBS			
Arrowleaf balsamroot	3479 ± 177 ^A	2777 ± 300 ^B	2294 ± 310 ^{aB*}
Spurred lupine	3498 ± 220 ^A	2767 ± 431 ^B	2416 ± 116 ^{B*}
GRASSES			
Bluebunch wheatgrass	2892 ± 234 ^A	2311 ± 374 ^{B*}	2181 ± 346 ^{aB*}
Idaho fescue	2716 ± 373 ^A	2372 ± 495 ^{A*}	2176 ± 503 ^{aA*}
Kentucky bluegrass	3027 ± 102 ^A	2291 ± 310 ^{B*}	2166 ± 281 ^{B*}
Mountain brome	3447 ± 221 ^A	2822 ± 197 ^A	2229 ± 134 ^{B*}
Needlegrasses	2969 ± 167 ^A	2146 ± 303 ^{B*}	1746 ± 210 ^{B*}
Sandberg bluegrass	2610 ± 326 ^{A*}	2104 ± 556 ^{aB*}	1865 ± 365 ^{B*}
WOODY BROWSE			
Aspen	3112 ± 560 ^{bA}	3005 ± 203 ^A	3081 ± 252 ^A
Curl-leaf mountain mahogany	2747 ± 332 ^A	2726 ± 206 ^{A*}	2878 ± 202 ^A
Mountain snowberry	3648 ± 130 ^A	3185 ± 317 ^{AB}	2928 ± 352 ^B
Snowbrush ceanothus	3057 ± 211 ^A	2833 ± 113 ^A	2862 ± 140 ^A
GOOD REQUIREMENTS ^c	2900	2900	2750

^aOutlier removed ($n = 5$).

^bJune 2000 aspen only ($n = 3$).

^cGood requirements are levels where cows with calves are assured to experience no, or virtually no, limitations in reproduction, survival, or growth from nutrition (Cook et al. 2004). Digestible energy good requirements are from Cook et al. (2004).

^{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 good requirement ($P < 0.05$) as tested by 1-tailed, 1-sample t test.

and then typically reaches concentrations below shrubs by the end of the growing season (Cook 1972). Digestible energy tends to be greater in herbaceous plants compared with shrubs across all stages of growth (Cook 1972). In our study woody browse generally contained highest levels of DE and CP by midsummer, 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 IVDMD of 75 ± 1% and 71 ± 1% in 1999 and 2000, respectively. Our findings agree with Dietz (1972) who reported that IVDMD for common snowberry (*S. albus*) was 71%, the highest of 6 species evaluated during the spring early leaf stage in the Black Hills of South Dakota.

Protein, vitamins, energy, fatty acids, water, and micro- and macrominerals are all essential; however, most wildlife nutritionists agree that energy and protein are likely the most limiting nutrients to wildlife populations (Spalinger 2000). Elk in our study area typically consumed more graminoids in spring and early summer (1998–2000 = 18%–60%) and then switched to a diet dominated by forbs in mid- to late summer (1998–2000 = 59%–78%; Beck

and Peek 2005). 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 good requirements for cow elk. Moreover, lupines (*Lupinus* spp.) constituted the major forb consumed (29%–41%), and snowbrush ceanothus was an important woody plant (0%–4%) consumed in mid- to late summers 1998–2000 (Beck and Peek 2005); these 2 forage species had the most reliable nutrient supplies across summers. Lupines contain alkaloids, which may deter herbivory; however, greatest consumption of spurred lupine in our study area occurred in mid- to late summer when total alkaloid levels were lowest, below potentially toxic levels (Beck and Peek 2005). Thus, 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, but this response was weak.

Understanding the ability of animals to obtain adequate nutrients through diet selection processes is a complex issue involving many factors such as nutrient availability, palatability, intake rates, and the ability of animals to detoxify or avoid toxic compounds. In another

TABLE 4. Ranges in mineral concentrations ($\mu\text{g} \cdot \text{g}^{-1}$ DM) 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 ranges in mean low and high concentrations across early summer, midsummer, and early fall, 1999 and 2000, on summer range in the Jarbridge Mountains, Nevada. Requirements and maximum tolerable levels for beef cattle are from National Research Council (1996) unless otherwise noted.

	Ca ($\mu\text{g} \cdot \text{g}^{-1}$)	K ($\mu\text{g} \cdot \text{g}^{-1}$)	Mg ($\mu\text{g} \cdot \text{g}^{-1}$)	Na ^a ($\mu\text{g} \cdot \text{g}^{-1}$)	P ($\mu\text{g} \cdot \text{g}^{-1}$)	S ($\mu\text{g} \cdot \text{g}^{-1}$)
FORBS						
Arrowleaf balsamroot	13,000–29,000	12,400–32,333	2300–2867	48–62	747–3467	1167–3567
Spurred lupine	13,667–22,333	8900–21,667	2400–4167	36–41	593–2867	860–2400
GRASSES						
Bluebunch wheatgrass	3233–8300	7100–19,333	1043–1233	33–43	420–2867	983–2100
Idaho fescue	3600–8533	9433–18,333	887–1233	24–39	970–2933	857–1567
Kentucky bluegrass	3567–5500	13,000–22,333	1007–1600	39–49	1233–3767	1297–2500
Mountain brome	3967–8733	19,333–40,000	1367–1933	32–40	1030–4567	1173–3833
Needlegrasses	4600–8967	9550–18,667	997–1200	27–41	507–2367	960–2233
Sandberg bluegrass	1867–9700	4967–18,667	947–1567	38–49	633–2167	823–1467
WOODY BROWSE						
Aspen ^b	9233–14,267	9933–18,000	1867–2300	N/A ^c	877–2500	980–1667
Curl-leaf mountain mahogany	6867–9267	4867–9533	1010–1500	18–52	1100–2367	703–1400
Mountain snowberry	5967–14,333	12,933–27,333	2133–3067	29–29	1333–3967	1100–2467
Snowbrush ceanothus	8400–9933	5233–12,333	1150–1667	18–36	997–3033	803–1867
REQUIREMENTS	1600–5800 ^d	6000–7000	1000–2000	600–1000	1700–3900 ^d	1500
MAXIMUM TOLERABLE LEVELS	20,000 ^d	30,000	4000	100,000 ^{de}	10,000 ^d	4000

^aSodium results from 1999 only. Sodium levels in all 2000 samples were below detectable levels.

^bAspen not collected in June 1999.

^cSodium values for aspen in 1999 were all below detectable levels.

^dNational Research Council (1984).

^eSodium chloride (table salt).

study we predicted that the highest probabilities of elk habitat selection in the Jarbidge Mountains were in areas near perennial streams with greater cover of aspen relative to conifer (Beck et al. 2005). These mesic foraging areas provide abundant, nutritious herbaceous forage to elk throughout summer as other forage sources senesce. However, even with high-quality herbaceous forage sources, elk diets consisted of 10%–35% and 10%–30% woody browse in spring and mid- to late summer 1998–2000, respectively (Beck and Peek 2005). Most deciduous woody plants contain tannins, a class of secondary plant compounds. Herbivores foraging on tannin-rich vegetation are faced with reduced protein digestion because tannins form insoluble complexes with proteins (Robbins et al. 1987, Beck and Reed 2001). Tannins restrict energy digestion in forages by binding with microbial enzymes in the rumen and forming indigestible complexes with cellulose and hemicellulose (Beck and Reed 2001). To counter the reduction in protein digestion, cervids have evolved large salivary glands that secrete tannin-binding salivary proteins, which prevent losses in protein digestion (Robbins et al. 1995). In addition, low to moderate concentrations of tannins in the rumen eliminate foaming properties of legume proteins (Beck and Reed 2001). Thus, elk selecting a diet high in lupines or other legumes may offset some of the negative effects of digesting leguminous forages by consuming tannin-rich woody browse.

Elk and other ungulates obtain nutrients that meet requirements by mixing plants with variable nutrient levels in diets (Hobbs and Swift 1985). Diet mixing, along with other mechanisms including cautious sampling and limited intake of novel foods, may enable herbivores to avoid toxicity of certain plant compounds (Freeland and Janzen 1974, Freeland 1991). Diet mixing may explain our inability to detect strong relationships between dietary incorporation of the 12 forage plants we evaluated and concentrations of CP and DE. For instance, mean species richness, or the average number of forage plants in elk fecal diets, in our study area from 1998 to 2000 was 34 in spring and 30 in summer (Beck and Peek 2005), which suggests elk actively selected mixed diets to meet nutritional requirements. In addition, elk in our study area had access to at least

400 species of vascular plants (Lewis 1975), providing a wide range of foraging options to obtain adequate nutrients. Declining grass quality likely requires cow elk on summer ranges in the Great Basin to select a mixed diet incorporating leguminous forbs and woody browse to obtain adequate nutrients as summers progress.

Sodium content in forages in our study was at best about 10% of requirements (National Research Council 1996). Ganskopp and Bohnert (2003) documented a similar ratio of Na relative to beef cattle requirements in 7 Great Basin grasses, and Alldredge et al. (2002) reported that average Na content in forages used by elk in northern Idaho was $\leq 10\%$ 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). In animals, Na is the principal cation of extracellular fluids and has several physiological functions including body fluid and osmolarity regulation, acid-base balance and tissue pH, muscle contraction, and nerve impulse transmission (Robbins 1993:44). Deficiency symptoms include reduced growth, loss of appetite, softening of bones, weakness and incoordination, gonadal inactivity, corneal keratinization, decreased plasma Na concentration, adrenal hypertrophy, impaired dietary energy and protein utilization, and decreased plasma and fluid volumes leading to shock and death (Robbins 1993:48). The ubiquitous spring salt drive 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).

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). With the exception of Na, adequate and tolerable macromineral levels were widely available in most forage plants we evaluated. It seems unlikely that elk in northeastern Nevada will suffer mineral deficiencies or toxicities leading to nutritional problems such as grass tetany.

MANAGEMENT IMPLICATIONS

Future increases in elk populations in the Great Basin should be monitored to ensure that key foraging communities and forage species are maintained and/or enhanced. Browsing from high-density elk populations results in declines in cover and productivity of structural woody species on summer and winter ranges including aspen (White et al. 1998, Dieni et al. 2000), snowbrush ceanothus (Tiedemann and Berndt 1972), true mountain mahogany (*C. montanus*; Turley et al. 2003), willows (*Salix* spp.; Singer et al. 1994), and Wyoming big sagebrush (*A. tridentata wyomingensis*; Singer and Renkin 1995). Because 60% (3/5) of the main community structural species (aspen, curl-leaf mountain mahogany, and snowbrush ceanothus) in our study area are nutritious foods, their reproduction, growth, and vigor should be monitored. Vegetation monitoring should be coupled with hunting seasons to reduce elk populations to prevent overuse of key woody communities. Overbrowsing of these woody plants will reduce the ability of Great Basin 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 and associated herbivory on localized areas. Managers therefore should decide 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-fall indicates that elk are increasingly challenged to satisfy good nutritional requirements as the supply of total forage that meets good requirements wanes. Thus, by early fall, foraging options that satisfy requirements are appreciably reduced. The extent to which quality of elk diets declines as overall forage quality declines is unknown, but it is clear that the potential for maintaining a relatively high density of elk at dietary quality levels that fulfill good requirements declines as summer progresses. Maintaining highly productive elk herds in the Great Basin requires that man-

agers (1) maintain plant communities with a diverse assemblage of grasses, forbs, and woody browse to provide for the nutritional needs of lactating cows and their growing calves and (2) manage elk and other ungulate populations at levels that do not promote overuse of key foraging communities.

ACKNOWLEDGMENTS

USDA Humboldt-Toiyabe National Forest; Nevada Division of Wildlife; Rocky Mountain Elk Foundation; Nevada Bighorns Unlimited; Elko Bighorns Unlimited; USDI Bureau of Land Management; National Fish and Wildlife Foundation; and the College of Natural Resources, the Department of Fish and Wildlife Resources, and the Cooperative Fish and Wildlife Research Unit, at the University of Idaho supported our research. J.S. Lewis, L.K. Peterson, C.S. Rudeen, and K.M. Smolski were invaluable field assistants. K.L. Launchbaugh facilitated use of the University of Idaho Rangeland Ecology and Management Laboratory for digestibility trials. We thank B.B. Davitt, K.A. Johnson, and J.J. Michal, Washington State University, for assistance with bomb calorimetry. C.J. Williams, University of Idaho, provided statistical advice. J.G. Cook, National Council for Air and Stream Improvement, La Grande, Oregon provided a helpful review of an earlier draft. We also thank the associate editor, J.L. Rachlow, and 2 anonymous reviewers for their insightful comments that improved our manuscript.

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. 2003. Elk summer range habitat, nutritional ecology, and carrying capacity in the Jarbidge Mountains, Nevada. Doctoral dissertation, University of Idaho, Moscow.
- 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. USDA Forest Service, Research Paper INT-RP-491, Ogden, UT.
- BECK, J.L., AND J.M. PEEK. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. *Rangeland Ecology and Management* 58: 135–147.
- BECK, J.L., J.M. PEEK, AND E.K. STRAND. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. *Journal of Wildlife Management* 70: in press.
- BECK, J.L., AND J.D. REED. 2001. Tannins: anti-quality effects on forage protein and fiber digestion. Pages 18–22 in K. Launchbaugh, editor, *Anti-quality factors in rangeland and pastureland forages*. Bulletin 73, Idaho Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow.
- BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York. 488 pp.
- 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*. USDA Forest Service, General Technical Report INT-1, Ogden, UT.
- COOK, J.G. 1990. Habitat, nutrition, and population ecology of two transplanted bighorn sheep populations in southcentral Wyoming. Doctoral dissertation, University of Wyoming, Laramie.
- _____. 2002. Nutrition and food. Pages 259–349 in D.E. Toweill and J.W. Thomas, editors, *North American elk: ecology and management*. Smithsonian Institution Press, Washington, DC.
- COOK, J.G., B.K. JOHNSON, R.C. COOK, R.A. RIGGS, T. DELCURTO, L.D. BRYANT, AND L.L. IRWIN. 2004. Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155. 61 pp.
- 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.
- 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.
- 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*. USDA Forest Service, General Technical Report INT-1, Ogden, UT.
- FREELAND, W.J. 1991. Plant secondary metabolites: biochemical coevolution with herbivores. Pages 61–82 in R.T. Palo and C.T. Robbins, editors, *Plant defenses against mammalian herbivory*. CRC Press, Boca Raton, FL.
- FREELAND, W.J., AND D.H. JANZEN. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* 108:269–289.
- GANSKOPF, D., AND D. BOHNERT. 2003. Mineral concentration dynamics among 7 northern Great Basin grasses. *Journal of Range Management* 56:174–184.
- HALL, E.R. 1946. *Mammals of Nevada*. University of California Press, Berkeley.
- HOBBS, N.T., AND D.M. SWIFT. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49: 814–822.
- 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, NJ.
- LEWIS, M.E. 1975. Plant communities of the Jarbidge Mountain complex, Humboldt National Forest. Report to Intermountain Region, USDA Forest Service, Ogden, UT. 22 pp.
- 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. USDA Forest Service, General Technical Report INT-250, Ogden, UT. 135 pp.
- MURIE, O.J. 1951. *The elk of North America*. Teton Bookshop, Jackson, WY.
- NATIONAL RESEARCH COUNCIL. 1984. Nutrient requirements of beef cattle. 6th edition. National Academy Press, Washington, DC. 90 pp.
- _____. 1996. Nutrient requirements of beef cattle, update 2000. 7th revised edition. National Academy Press, Washington, DC. 232 pp.
- NEVADA DIVISION OF WILDLIFE. 1997. Nevada elk species management plan. Nevada Division of Wildlife, Reno. 83 pp.
- _____. 2000. Sub-plan for elk management in the Jarbidge Mountains, Nevada. Nevada Division of Wildlife, Reno. 4 pp.
- OEHLERT, G.W. 2000. *A first course in the design and analysis of experiments*. W.H. Freeman, New York. 659 pp.
- 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, DC.
- 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*. USDA Forest Service, Miscellaneous Publication 1147, Flagstaff and Tempe, AZ.
- ROBBINS, C.T. 1993. *Wildlife feeding and nutrition*. 2nd edition. Academic Press, San Diego, CA. 352 pp.
- ROBBINS, C.T., T.A. HANLEY, A.E. HAGERMAN, O. HJELJORD, D.L. BAKER, C.C. SHWARTZ, AND W.W. MAUTZ. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98–107.
- ROBBINS, C.T., D.E. SPALINGER, AND W. VAN HOVEN. 1995. Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? *Oecologia* 103:208–213.
- SAS INSTITUTE. 2001. *SAS/STAT user's guide*. Release 8.2. SAS Institute, Incorporated, Cary, NC.
- 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.
- SINGER, F.J., 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.

- SPALINGER, D.E. 1980. Mule deer habitat evaluation based upon nutritional modeling. Master's thesis, University of Nevada, Reno.
- _____. 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, NJ.
- SVEJCAR, T., AND M. VAVRA. 1985. The influence of several range improvements on estimated carrying capacity and potential beef production. *Journal of Range Management* 38:395–399.
- TIEDEMANN, A.R., AND H.W. BERNDT. 1972. Vegetation and soils of a 30-year deer and elk enclosure in central Washington. *Northwest Science* 46:59–66.
- 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. 104 pp.
- TURLEY, D., B.A. ROUNDY, AND S.C. WALKER. 2003. True mountain mahogany community and shrub size responses to browsing. *Journal of Range Management* 56:600–607.
- USDA FOREST SERVICE. 1981. Environmental assessment for the release of elk into the Jarbidge Mountains, Elko County, Nevada. USDA Forest Service, Humboldt National Forest, Elko, NV. 25 pp.
- VALENTINE, J.F. 1990. Grazing management. Academic Press, San Diego, CA. 533 pp.
- VAN SOEST, P.J. 1994. Nutritional ecology of the ruminant. 2nd edition. Cornell University Press, Ithaca, NY. 476 pp.
- 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, NJ.

Received 5 April 2004
Accepted 16 February 2005