Research Article

Estimates of Elk Summer Range Nutritional Carrying Capacity Constrained by Probabilities of Habitat Selection

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Abstract

We used habitat-selection data from a reintroduced population of elk (Cervus elaphus) in northeastern Nevada, USA, to develop a resource-selection function to adjust nutritional carrying capacity estimates. Constrained estimates provide population levels that minimize overuse of key foraging communities. We estimated economic nutritional carrying capacity (I_{NCC}) for 236-kg lactating cow elk in autumn 1999 and 2000 to reflect expected animal performance under maintenance (2,550 kcal/kg DM) and good (2,750 kcal/kg DM) levels of standing digestible energy. We used our resource-selection function to redistribute I_{NCC} densities (RSFD) for aspen (Populus tremuloides), conifer, curl-leaf mountain mahogany (Cercocarpus ledifolius), sagebrush (Artemisia spp.)–herb, and snowbrush ceanothus (Ceanothus velutinus) cover types across the summer range and then adjusted original I_{NCC} estimates according to these RSFD when expected densities exceeded original I_{NCC} estimates. Maintenance performance I_{NCC} estimates were 2,533 cow elk (95% CI: 1,327–3,739) in 1999 and 1,655 (95% CI: 886–2,424) in 2000. Good performance I_{NCC} estimates were 2,264 cow elk (95% CI: 1,150–3,378) in 1999 and 1,100 (95% CI: 384–1,816) in 2000. The best habitat model provided evidence that forage availability and distance to water influenced habitat selection. Adjustments in I_{NCC} for 1999 and 2000 and at both performance levels corresponded to decreases of 18–35% in original I_{NCC} estimates. Decreases were attributed to more cow elk predicted by RSFD to be in aspen, conifer, and sagebrush–herb cover types than predicted by I_{NCC}. Each year, RSFD predicted that fewer elk would use mahogany and snowbrush cover types than original I_{NCC} models. The adjusted carrying capacity estimates provided population levels that should avoid appreciable alteration of aspen, conifer, and sagebrush–herb communities while ensuring nutritious resources during lean periods. Our paper provides a critical refinement for nutritional carrying capacity models through incorporating prediction of animal selection of nutritional resources. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):283–294; 2006)

Key words

aspen, Cervus elaphus*, elk, habitat alteration, habitat selection, Nevada, nutritional carrying capacity,* Populus tremuloides*, resource selection functions.*

A fundamental objective of wildlife management is to estimate carrying capacity, or the number of animals that the resources of an area can support over specific periods. Nutritional carrying capacity relates an animal's specific nutritional requirements to the availability of those nutrients in 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 animal modeled are needed to model 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). Interspecific interactions including risk of predation by predators (White et al. 1998, Ripple and Beschta 2003), as well as the physical presence of conspecifics such as livestock and effects of their forage-consumption patterns (Mackie 1970, Clegg 1994) may also cause wild ungulate densities to differ among habitats of varying quality.

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 harvest. 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). Browsing pressure from high-density elk (*Cervus elaphus*) 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, 1998, Singer and Renkin 1995; White et al. 1998; Dieni et al. 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

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ecosystem components (deCalesta and Stout 1997, Weisberg et al. 2002). For example, simulation modeling for elk in North Park, Colorado, USA, indicated that 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). Nevertheless, nutritional carrying capacity models considering the influence of habitat use have not been developed.

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 compelling model to evaluate relationships between summer nutritional carrying capacity and habitat selection 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, 2004). In summer, cows with calves must balance habitat selection between areas that provide security for neonates and high-quality forage for milk production and accumulation of sufficient body reserves for future reproduction (Geist 1982).

Our objective was to develop a nutritional carrying capacity model for elk summer range to estimate population levels that do not alter vegetation conditions. We use data from an elk population reintroduced into northeastern Nevada to demonstrate how nutritional carrying capacity estimates are constrained by habitat-selection patterns. We designed our study 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} estimates with the resource-selection function from the best model 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 alter important foraging communities. Our approach to modeling nutritional carrying capacity 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) elk habitat use will be below levels that can appreciably alter resource conditions or plant succession; 3) elk and other ungulates have equal availability to forage resources on the given unit of land evaluated in carrying capacity equations; 4) these models are applicable in the absence of large-scale disturbances such as substantial wildfire or severe prolonged drought; 5) disease and predation 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

Our study area comprised Nevada Division of Wildlife (NDOW) Hunt Unit 072 (41°30' to 42°00'N and 115°00' to 115°30'W) in northeastern Nevada, USA (Fig. 1). Hunt Unit 072 consisted of 1,665 km² with elevations ranging from 1,633 to 3,287 m. We delineated all area ≥2,135 m as elk summer range (Fig. 1) because
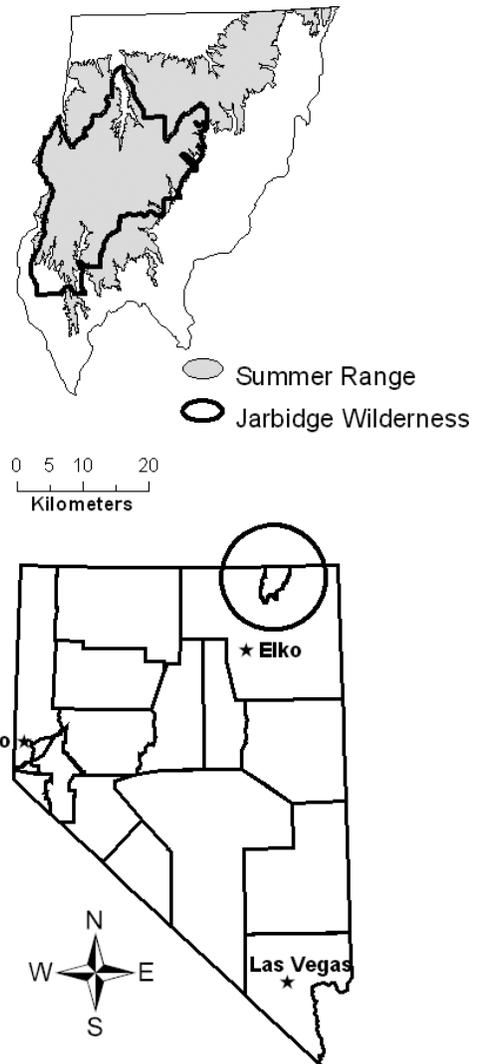
Figure 1. Study-area location map, Jarbidge Mountains, Nevada, USA, 1998–2001. The study area encompassed the 1,665 km² Nevada Division of Wildlife Hunt Unit 072. Summer range was delineated as all area ≥2,135 m and included 802 km². The 392 km² U.S. Forest Service Jarbidge Wilderness Area comprised 49% of the summer range.

93% of cow elk located on radiotelemetry flights across summers 1998–2001 were found above this elevation. Summer range included 802 km² (48%) of the study area and was administered by the U.S. Forest Service (92%), Bureau of Land Management (5%), and private ownership (3%). The 392-km² U.S. Forest Service Jarbidge Wilderness comprised most of the Jarbidge Mountains and 49% of the summer range (Fig. 1). Watersheds in the north of the study area drain to the Snake River and those in the south drain to the Great Basin (U.S. Forest Service 1981).

Snowpack accumulated from late fall through mid-spring provides most moisture for plant growth in the study area. Snow water equivalents on 1 April at weather stations at Draw Creek (2,300 m) in the south and Pole Creek Ranger Station (2,540 m) in the north were 126, 88, and 104%, and 94, 91, and 90% of 30-year (1971–2000) averages (Draw Creek, 297 mm; Pole Creek, 523 mm) in 1998, 1999, and 2000, respectively. Average monthly temperatures (C) from June through October, 1998, 1999, and

2000 were 12, 11, and 14 at Draw Creek (1991–2000 $\bar{x} = 12$), and 10, 10, and 11 at Pole Creek (1991–2000 $\bar{x} = 10$). June through October 1998, 1999, and 2000 cumulative precipitation (cm) was 14, 10, and 4 at Draw Creek (1985–2000 $\bar{x} = 10$), and 23, 10, and 5 at Pole Creek Ranger Station (1985–2000 $\bar{x} = 14$).

Mountain big sagebrush (*A. t. vaseyana*) and little sagebrush (*A. arbuscula*) interspersed with herbaceous meadows and snowbank associations formed a matrix between forested communities. Forested communities included aspen, curl-leaf mountain mahogany (*Cercocarpus ledifolius*), snowbrush ceanothus (*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 to 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 (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), cattle, and domestic sheep. Livestock were grazed on 11 sheep, 27 cattle, and 1 common-use summer and early-autumn allotments within the study area. Elk calves per 100 cows ratios from 1 July to mid-September 1998–2000 averaged 52 (range = 32–57), 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 (Beck 2003). Management 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 lactating cow elk in autumn to reflect expected animal performance under reasonable ranges in digestible energy (DE). Elk nutritional requirement calculations have typically considered 236 kg to be an average size for elk cows (Nelson and Leege 1982, Cook 2002). Autumn, which began on 1 September, was delineated by weather data in our study area, with a maximum length of 76 days (Beck 2003). We assumed nutrition was adequate to satisfy requirements for calf growth and fat accretion in cows over spring/summer months prior to 1 September. The period from 1 September through 15 November marks a period of transition from high to a lower nutritional demand level; therefore, the range in DE levels we examined represent averages for maintenance and good performance across this period (Cook et al. 2004). 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. In addition, maintenance performance will likely only support low-to-moderate calf growth (Cook et al. 2004). Good performance (2,750 kcal/

kg) represented levels in which cows with calves would be assured to experience no (or virtually no) limitations in reproduction, survival, or growth from nutrition (Cook et al. 2004). 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 $I_{NCCi} \pm t_{\alpha/2,\ n-1} \times SE$.

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

where $\widehat{I_{NCC_i}}$ = economic nutritional carrying capacity in autumn of year *i*, $\widehat{SDE_{jm}}$ = mean standing digestible energy (kcal/ha) for forage item *j* in cover type *m*, $\widehat{Use_{jm}}$ = 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 $\widehat{I_{NCC_i}}$ was approximated as the variance of a product (Goodman 1960):

$$\widehat{V_{I_{NCC_i}}} = \sum_{j=1}^{n} \sum_{m=1}^{5} C_{jm}^2 \left(\hat{V}[(\widehat{SDE_{jm}})(\widehat{Use_{jm}})] \right) \tag{2}$$

where $C_{jm}^2 = \left(\frac{Area_{jm}}{DMI \times DER \times Days_i} \right)^2$, and

$$\hat{V}[(\widehat{SDE_{jm}})(\widehat{Use_{jm}})] = (\widehat{SDE_{jm}^2})\left(\hat{V}(\widehat{Use_{jm}}) \right)$$
$$+ (\widehat{Use_{jm}^2})\left(\hat{V}(\widehat{SDE_{jm}}) \right)$$
$$- \left(\hat{V}(\widehat{SDE_{jm}}) \right)\left(\hat{V}(\widehat{Use_{jm}}) \right)$$

We based carrying capacity on conditions in 1999 and 2000 in 5 general cover types covering our study area. Cover-type availability was aspen (121 km^2), conifer (86 km^2), mahogany (158 km^2), sagebrush–herb (415 km^2), and snowbrush (22 km^2). Nutritional parameters incorporated in our carrying capacity model were 1) dry matter intake (DMI) for lactating 236-kg cow elk in mid-autumn estimated at 6.9 kg/day (Cook et al. 2004), and 2) DE content (kcal/kg) required to provide maintenance performance (2,550) and good performance (2,750) for lactating 236-kg cow elk in early autumn (Cook et al. 2004); 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). Specifically, we estimated SDE for 15 forage species or categories found among the 5 cover types and identified as important forages in elk feeding sites and through microhistological fecal analysis (Beck 2003, Beck and Peek 2005*a*). Forage species we selected were perennial forbs and perennial graminoids in aspen, conifer, mahogany, and sagebrush–herb cover types; aspen in aspen cover; mahogany in mahogany cover; snowbrush in snowbrush cover; and mountain snowberry (*Symphoricarpos oreophilus*) representing the understory shrub component selected by elk in aspen, conifer, mahogany, and sagebrush–herb cover types. We constrained availability of SDE to elk in 3 ways to represent foraging conditions in autumn on summer range: 1) initial SDE availability was residual SDE following summer livestock and wildlife grazing; 2) by further

reducing available SDE according to estimated use by elk in feeding sites; and 3) by adjusting estimated proportions of use in elk feeding sites to reflect nutrient concentrations in mixed diets (Hobbs and Swift 1985).

Following removal of livestock in late September/early October 1999 and 2000, we estimated residual standing crop of herbs and current annual growth of shrubs with a double-sampling technique (Bonham 1989) in aspen and mahogany cover types in 225-m² plots and residual current annual growth of snowbrush in snowbrush cover types along paired, 75-m transects (Beck 2003). We obtained early autumn DM forage production estimates for conifer and sagebrush–herb cover types from other sources (Jensen et al. 1988, U.S. Forest Service 1988) and adjusted these estimates to represent use in sagebrush and conifer cover types based on Humboldt-Toiyabe National Forest allowable-use levels for nonriparian rangeland of 60% for herbs and 50% for current annual growth of shrubs in deferred rotation allotments.

We estimated DE content in forage samples collected in 3 grazing allotments in early autumn 1999 and 2000 (Beck and Peek 2005b). We averaged DE values among forage species within cover types to reflect average expected DE availability in common forage species in each cover type. We averaged DE content of arrowleaf balsamroot (Balsamorhiza sagittata) and spurred lupine (Lupinus caudatus) to represent perennial forb energetic value in aspen, conifer, mahogany, and sagebrush–herb cover types. We calculated mean DE values for major woody browse species in each cover type on a species-specific basis, and we evaluated DE content for aspen and snowberry in aspen cover, mahogany and snowberry in mahogany cover, snowbrush in snowbrush cover, and snowberry in sagebrush–herb and conifer cover types. We averaged DE estimates for Kentucky bluegrass (Poa pratensis), mountain brome (Bromus marginatus), and needlegrass (Achnatherum spp.) to represent grass energy in aspen cover. We averaged bluebunch wheatgrass (Pseudoroegneria spicata), mountain brome, and needlegrass DE to represent energy content of grasses in conifer and mahogany cover types. We averaged DE in bluebunch wheatgrass, Idaho fescue (Festuca idahoensis), Kentucky bluegrass, mountain brome, needlegrass, and Sandberg bluegrass (P. secunda) to calculate energetic content of grasses in sagebrush–herb cover.

Proportions of forage items eaten by elk in cover types (Use$_{jm}$) represent mean use of perennial forbs, perennial graminoids, and woody browse observed at elk feeding sites. Estimated proportionate elk use in forested communities was 0.101 (SE = 0.029), 0.009 (SE = 0.003), and 0.045 (SE = 0.022) for perennial forbs, perennial graminoids, and woody browse, respectively. In sagebrush–herb communities, estimates were 0.091 (SE = 0.018), 0.013 (SE = 0.003), and 0.035 (SE = 0.017) for perennial forbs, perennial graminoids, and woody browse, respectively (Beck 2003). Specific methods for estimating forage use in feeding sites are found in Beck and Peek (2005a). We used Hobbs and Swift's (1985) nutritional carrying capacity algorithm to adjust estimated proportions of forage used in mixed diets for elk selecting diets at maintenance and good performance levels (Cook et al. 2004). Accordingly, we 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). Consequently, we removed

perennial graminoids from aspen, conifer, mahogany, and sagebrush–herb cover types in the 2000 maintenance performance I$_{NCC}$ model and from the 1999 and 2000 good performance I$_{NCC}$ models, after the algorithm indicated that DE content in graminoids was too low to be incorporated into a mixed diet meeting cow elk energy requirements in autumn. Appendices in Beck (2003) outline portions of our nutritional carrying capacity model including development of our cover-type availability map, methods to estimate SDE, energetic requirements of elk, and delineation of autumn.

Elk Group Habitat Selection

Nevada Division of Wildlife personnel captured 10 cow elk in 1998 and 7 cow elk in 2000 on winter range with netguns shot from helicopters to facilitate attachment of VHF radiocollars (Telemetry-Electronics Consultants, Mesa, Arizona). Radio-marked cows provided us locations of elk groups composed primarily of cows, calves, and yearling bulls. Nevada Division of Wildlife used Cessna 206 Turbo fixed-wing aircraft to locate cow elk groups on 19 relocation flights (1998 = 3; 1999 = 7; 2000 = 7; 2001 = 2) 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. An NDOW biologist determined group locations through ocular observations or by strength of signal of collared elk and recorded locations 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, Redlands, California, 1992–2002) to derive Universal Transverse Mercator (UTM) coordinates.

From 1998 to 2000, we located radiocollared 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 (including collared cows) from ground counts by the number of collars located on each flight. We divided these products by the estimated population of cows and yearling bulls and then multiplied by 100 to calculate the percentage of the cow and yearling bull population located on each flight. Nevada Division of Wildlife minimum population estimates for cows and yearling bulls were 202 (0.623 of total N) in 1998; 198 (0.614 of total N) in 1999; and 185 (0.682 of total N) in 2000 (J. Williams, NDOW, personal communication).

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. Spatial independence of all groups was not clearly ascertainable during location flights. To address this issue we assessed independence of groups located on each of the 19 aerial location flights following 3 criteria: 1) elk group locations >4 km apart were deemed to be independent; 2) elk groups <0.5 km were considered to function as single groups, thus single-collared elk were combined with the nearest location

of groups with multiple-collared animals, or when 2 locations of single-collared cow elk were <0.5 km apart we randomly placed 1 elk with the second elk; and 3) for elk groups 0.5–4 km apart, we evaluated viewsheds (Pierce et al. 2004) reasoning that groups in areas where topography did not block their view may have functioned as a single group. We constructed viewsheds from our digital elevation model in ArcView 3.3 for an elk standing at each group location with its head at a height of 1.5 m. After examining these topographical viewsheds we used our cover-type availability map to assess whether forested cover types screened the view of each elk group location from the other groups located on each flight. We subsequently combined groups 0.5–4 km apart located on the same flights that were not screened by topography or vegetation into single groups. This protocol resulted in reducing our set of independent groups from 136 to 127.

Our sampling approach followed Design 2 of Thomas and Taylor (1990), where use was identified for each individual group, and availability was defined for the population at each flight. We placed noncontiguous buffers with 2.3-km radii around 127 independent elk groups located during aerial flights. Buffer radii represented the median distance collared cow elk moved between relocation flights and hence provided us an analysis region that encompassed habitats selected during day and night even though elk were located during morning hours (Beyer and Haufler 1994). We evaluated successive distances individual cows moved between flights because group membership frequently changed. The distribution of movements was skewed right, indicating the need for use of nonparametric methods. Consequently, we used the median distance moved to represent 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 (1,678 ha) thus captured 50% of the movement distances of individual elk between successive relocation flights (Boyce et al. 2003). The area circumscribed by these buffers was analogous to 50% elk group home ranges, providing an analysis region to evaluate selection of home ranges within our study area comparable 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.

We weighted habitat variables at each elk group location by the number of radiocollared elk in each group, and we averaged habitat variables at elk locations by the 19 relocation flights. We also averaged random locations according to 19 random groupings of noncontiguous buffers equal to the number of elk groups located during each flight. During each flight, we identified use for each elk group within noncontiguous buffers, while we evaluated availability 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, nonoverlapping 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, Boyce et al. 2003). We clipped buffers that extended past the summer-range boundary within the extent of the summer range to set all habitat evaluations within the same area. In addition, the large size of our buffers overcame error and bias in locations while providing an analysis of the mosaic of habitats encountered on the summer range (Rettie and McLoughlin 1999).

Geographic Data

We obtained data for our habitat-selection model from geographic data coverages. We used ERDAS IMAGINE 8.5 (ERDAS®, Inc., Atlanta, Georgia) to create a cover-type availability map (overall map accuracy = 90%, kappa statistic = 0.82) representing composition of aspen, conifer, mahogany, sagebrush–herb, and snowbrush on the summer range. We created our cover type map from 3 Landsat 7 ETM+ scenes (24 Sep 1999 [Path 41, Row 31], 15 Sep 2000 [Path 40, Row 31], and 17 Oct 2000 [Path 40, Row 31]) with ground resolution of 30 m (Homer et al. 2002; map projection, UTM Zone 11; datum, NAD 1927). We selected autumn Landsat scenes because differences in spectral reflectance between forested and sagebrush–herb communities were more pronounced. We created our cover-type map 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 1 continuous map without cloud and shadow.

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 compensated for the unit-sum constraint in multivariate analysis of variance (MANOVA) by computing natural log ratios of cover types (Aebischer et al. 1993) in buffers with the focal sum function in ArcGIS 9.0 (Environmental Systems Research Institute, 1982–2004). We computed natural log ratios 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 ($X4$). We incorporated aspen 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).

We obtained our roads coverage from a U.S. Census Bureau 2000 Tiger® digital line-graph file at 1:100,000 scale. Because all roads were gravel and unimproved, we evaluated them as 1 road category. Our 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). We evaluated distances (km) from elk group and random buffer centers to nearest road and perennial stream arcs with the near command in ArcGIS 9.0.

We spatially analyzed raster data in the ArcGIS 9.0 GRID module. We used a 30-m USGS digital elevation model to compute elevation (m), slope (%), and aspect. We tabulated mean elevation and mean percent slope in each 2.3-km buffer. We arcsine square-root transformed slope proportions to meet assumptions of normality and equal variance. We reclassified aspect 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 Jeffery 1964, Skovlin et al. 2002).

Habitat Selection Modeling

We used a 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 assessed variables to meet the assumptions of MANOVA including multivariate normality and covariance homogeneity prior to the analysis. Consequently, we transformed single cover-type proportions with the arcsine square-root transformation to meet assumptions. Predictor variables considered in MANOVA modeling were 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 cover in each buffer, distances (km) from buffer centers to the nearest perennial stream (H2O) and road (ROAD), mean elevation (ELEV), mean percent slope (SLOPE), and percentage of cool aspect in each buffer (COOL). Prior to modeling, we assessed multicollinearity between variables with a Pearson's correlation matrix and removed 1 variable from each correlated pair when $r \geq 0.60$; variables correlated with >1 other variable were preferentially removed (PROC CORR; SAS Institute 2001). Removing correlated variables reduced the set of habitat variables included in our models to MAHOG, X2, X4, ROADS, H2O, and COOL. We report descriptive statistics and used paired t-tests to evaluate differences in habitat predictor variables between elk group locations and available habitat represented through random locations (PROC T-TEST; SAS Institute 2001).

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). We used nontransformed variables to predict elk habitat selection because logistic regression does not assume multivariate normality and covariance homogeneity in predictor variables. In addition, nontransformed variables provided clarity in interpreting our results. Our logistic regression model provided a fit to habitat predictor variables where the dependent data were 1 for used units and zero for available units (Boyce and McDonald 1999). Through logistic regression we examined 21 models based on 6 alternative explanations concerning elk habitat selection in our study area: 1) forage, 2) forage and distance to roads, 3) forage and topography, 4) forage and distance to water, 5) distances to roads and water, and 6) topography and distances to roads and water. We evaluated model fit in 2 and 3 parameter models to avoid overfitting models with too many parameters.

We assessed the strength of evidence for each logistic regression model with Akaike's Information Criterion for small samples (AIC$_c$). We selected the model with the lowest AIC$_c$ value as the best-fitting model, and we used Δ_i, the difference between AIC$_c$ for the best model and AIC$_c$ for the ith candidate model to identify models competing with the best model. We followed the convention that models with $\Delta_i \leq 2$ were competitive with the best model, and models with $\Delta_i > 10$ were poorly supported (Burnham and Anderson 2002). Akaike weights (w_i) allowed us to assess the weight of evidence in favor of each model (Burnham and Anderson 2002). We report rankings for the top 7 candidate models.

We used the best logistic regression model to estimate resource-selection function ($w[\mathbf{x}]$) coefficients based on a vector $\mathbf{x}$ of habitat-predictor variables. Resource-selection functions are probabilities proportional to use of resource units (Manly et al. 2002). In this model, exp is the natural exponent, and $\exp(\beta_i)$ are interpretable as odds ratios (Boyce et al. 2003).

$$w(\mathbf{x}) = exp(\beta_o + \beta_1 x_1 + \beta_2 x_2) \tag{3}$$

We applied the resource-selection function from the best model to our 30-m resolution cover-type availability map to derive a spatially explicit habitat-selection grid for 2.3-km buffer sizes. We used the moving window operation in ArcGIS 9.0 GRID module 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 9.0 GRID module to substitute 1 in cover-type ratio calculations when the value of conifer was zero within a moving window to avoid computational problems inherent when dividing with zeroes. The moving window operation considered 18,627 pixels (77×30 m $= 2,310$ m radius) at the 2.3-km scale. Within these moving window regions, we computed all grid calculations associated with making our resource-selection function spatially explicit.

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

$$U(\mathbf{x}_i) = w(\mathbf{x}_i)A(\mathbf{x}_i)/\sum w(\mathbf{x}_j)A(\mathbf{x}_j) \tag{4}$$

We obtained density, $D(\mathbf{x}_i)$, of 236-kg cow elk under maintenance and good performance levels in each cover type 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):

$$D(\mathbf{x}_i) = I_{NCCi} \times U(\mathbf{x}_i)/A(\mathbf{x}_i) \tag{5}$$

We examined differences between yearly I$_{NCC}$ estimates at both performance levels redistributed as RSFD in each cover type as I$_{NCC}$ − RSFD, when RSFD exceeded original I$_{NCC}$ estimates. We adjusted our estimates in this manner to avoid estimates that would promote overuse of forage in communities.

We applied the logistic regression probability function to our 30-m resolution cover-type 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.

$$\tau(\mathbf{x}) = exp(\beta_o + \beta_1 x_1 + \beta_2 x_2)/(1 + exp[\beta o + \beta_1 x_1 + \beta_2 x_2]) \tag{6}$$

We then tabulated the area of each cover type within 6 probability classes (0.00–0.10, 0.10–0.25, 0.25–0.50, 0.50–0.75, 0.75–0.95, 0.95–1.00) on our spatially explicit habitat selection probability grid to depict the distribution of predicted use of cover types by elk.

Cross-Validation Procedure

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. We used cross-validation iterative procedures to model 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. We sorted predicted probabilities and placed them into 10 groups with the first 9 containing 4 values and the last containing 2 values. We ranked bins according to increasing probabilities of elk presence. Within each of the 10 groups, we calculated the ratio of observations with observed elk occurrence. We calculated a Spearman's rank correlation (PROC CORR; SAS Institute 2001) between bin ranks and cross-validated prediction ratios of elk presence. A strong positive correlation would indicate that 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 (1 Sep–23 Oct) and autumn 2000 to be 76 days (1 Sep–15 Nov) in length. Among the 5 cover types, 11 elk forage species or forage categories comprised energetic intake in the 2000 maintenance I_{NCC} model and the 1999 and 2000 good performance I_{NCC} models, while energetic intake in the 1999 maintenance I_{NCC} model consisted of 12 species or categories (Appendix A). Perennial forbs in the sagebrush–herb cover type composed the highest fraction of total energetic intake (39.2–41.2%) in the 1999 and 2000 maintenance I_{NCC} models and the 1999 good I_{NCC} performance model. Snowbrush formed the highest percentage of total energetic intake (28.7%) in the 2000 good performance model (Appendix A).

Maintenance performance I_{NCC} estimates for 236-kg lactating cow elk were 2,533 (95% CI: 1,327–3,739) in 1999 and 1,655 (95% CI: 886–2,424) in 2000. Good performance I_{NCC} estimates for 236-kg lactating cow elk were 2,264 (95% CI: 1,150–3,378) in 1999 and 1,100 (95% CI: 384–1,816) 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 good performance were $2.8/km^2$ in 1999 and $1.4/km^2$ in 2000.

Elk Group Habitat Selection

One cow collared in 1998 summered outside of the study area each year and was thus not included in our habitat-selection analysis. We obtained 175 locations from 16 radiomarked elk cows (mean locations per cow = 10.1 [range = 1–19]) on 19 flights across summers 1998–2001. Of these locations, 162 of 175 (93%) occurred on summer range. Individual elk cows (8.5 ± 0.7 [±SE] individual elk located/flight) provided locations of 127 independent elk groups (6.7 ± 0.7 elk groups/flight) on summer range. We located cow elk groups on the ground following 15 flights in summers 1998–2000. On average, ground counts for cow elk groups located with radiocollared cows represented 56 ± 10% of combined adult cow and yearling bull estimates from 1998 to 2000. Groups located in early June were smallest (6–10%), reflecting the period when cows separate to calve or attend to neonates. However, by mid- to late August, cow elk nursery groups located with radiomarked elk cows represented 96–111% of estimated adult cows and yearling bulls in the population.

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 $\Lambda = 0.19$, $F_{18,28} = 1.28$, $P = 0.270$). Composition of cover types in 2.3-km elk buffers consisted of higher aspen and snowbrush and less conifer than composition of cover types in random 2.3-km buffers (Table 1). Elk groups used habitats closer to perennial streams and roads than at random (Table 1). Elk groups selected habitats with lower slopes than at random. There was no difference between elk-used and random locations for cool aspect, elevation, mahogany cover, or sagebrush–herb cover (Table 1).

The best logistic regression model, which included X2 and H2O, provided evidence in support of forage availability and distance to water influencing habitat selection (Fig. 2). No other models were competitive ($\Delta AIC_c \geq 12.355$) with the best model, and the predictor variables in the best model (X2 or H2O) were included in the other 6 top candidate models (Table 2). The parameter estimate for H20 at the km scale was −12.537 (SE = 5.585). By dividing the parameter estimate and its SE by 10, we rescaled H2O to the hectometer scale (100 m); at this scale, the odds for cow elk groups selecting habitat were 3.5 (95% CI: 1.2–10.5) times greater for each 100 m decrease in distance to a perennial stream. The parameter estimate for X2 was 8.694 (SE = 4.013). To evaluate odds of elk habitat selection for each 10% increase in aspen to conifer cover on the summer range, we rescaled by dividing the X2 parameter estimate and SE by 10. The odds for cow elk groups selecting habitat were 2.4 (95% CI: 1.1–5.2) times more likely with each 10% increase in the ratio of aspen to conifer cover. Our cross-validation analysis indicated that the best model was a strong, positive predictor of elk habitat selection ($r_s = 0.86$, $P = 0.002$, $n = 10$).

Distribution of each cover type among probability of use classes was bimodal (Fig. 3). This bimodality reflects 1) the low probability of selection ($P \leq 0.10$) for cover occurring far from water and in areas with more conifer cover relative to aspen cover, and 2) the high probability of selection ($P \geq 0.95$) for cover close to water in areas with high aspen cover relative to conifer cover. Conifer had the highest proportion of area within the lowest probability class ($P = 0.00$–0.10), followed by mahogany, aspen, sagebrush–herb, and snowbrush. Sagebrush–herb had the highest proportion of area in the highest probability of use class ($P = 0.95$–1.00), followed by snowbrush, aspen, mahogany, and conifer (Fig. 3).

Nutritional Carrying Capacity Adjusted with Resource-Selection Function Densities

Maintenance performance I_{NCC} estimates adjusted with RSFD resulted in 511 fewer elk in 1999 (adjusted $I_{NCC} = 2,022$; density = $2.5/km^2$) and 303 fewer elk in 2000 (adjusted $I_{NCC} = 1,352$; density = $1.7/km^2$), corresponding to 20 and 18% decreases in original 1999 and 2000 maintenance performance I_{NCC} estimates, respectively (Table 3). Maintenance performance I_{NCC} differences in 1999 were attributed to an increase of 451 cow elk in aspen cover and 60 cow elk in sagebrush–herb cover above I_{NCC} estimates as predicted with RSFD. The difference between 2000 I_{NCC} maintenance performance estimates and RSFD was a

Table 1. Descriptive statistics for habitat predictor variables in 2.3-km buffers around elk and random locations, Jarbidge Mountains, Nevada, USA, summers 1998–2001. Elk locations were weighted by number of radiocollared cows in each group and represent averages from 127 independent elk groups on $n = 19$ flights. Elk locations were compared to 127 random, paired locations averaged by $n = 19$ groups in conditional fixed-effects logistic regression modeling. Paired t-tests evaluated differences between habitat predictor variables at elk group and random locations.

Predictor variables	Elk groups		Random locations			
	$\bar{x}$	SE	$\bar{x}$	SE	t	P
Cover types (%)						
Aspen	16.3	0.3	13.7	0.4	5.33	<0.001
Conifer	8.4	0.6	11.5	0.6	−4.53	<0.001
Mahogany	17.1	0.5	17.6	0.6	−1.00	0.330
Sagebrush–herb	54.0	0.9	54.0	1.4	−0.01	0.991
Snowbrush	4.2	0.2	3.1	0.2	5.11	<0.001
Landscape features[a]						
Stream (km)	0.5	0.1	0.9	0.1	−4.47	<0.001
Road (km)	1.9	0.2	2.5	0.2	−2.83	0.011
Topography						
Cool aspect (%)[b]	48.7	1.3	50.0	1.5	−1.40	0.178
Elevation (m)[c]	2,444	14	2,465	16	−1.65	0.116
Slope (%)[d]	32.6	0.5	35.8	0.8	−4.64	<0.001

[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.

prediction of 253 cows in aspen cover, 4 in conifer cover, and 46 cows in sagebrush–herb cover above I_{NCC} estimates (Table 3).

Good performance I_{NCC} estimates adjusted with RSFD resulted in 434 fewer elk in 1999 (adjusted I_{NCC} = 1,830; density = 2.3/km^2) and 384 fewer elk in 2000 (adjusted I_{NCC} = 716; density = 0.9/km^2). Adjusted estimates corresponded to 19 and 35% decreases in original 1999 and 2000 good performance I_{NCC} estimates, respectively (Table 3). Good performance I_{NCC} differences in 1999 were attributed to an increase of 406 cow elk in aspen cover, 11 in conifer cover, and 17 cow elk in sagebrush–herb cover greater than I_{NCC} estimates as predicted with RSFD. The difference between 2000 I_{NCC} good performance estimates and predicted RSFD was 163 cows in aspen cover, 10 in conifer cover,

and 211 cows in sagebrush–herb cover above I_{NCC} estimates (Table 3).

Discussion

Our approach of using resource-selection functions to adjust nutritional carrying capacity estimates met our objective of providing population levels that should minimize alteration of key foraging communities. In our study, the number of elk using aspen, conifer (in 3 of 4 cases), and sagebrush–herb cover types were predicted to be in excess of nutritional resources, while elk densities predicted with the resource-selection function indicated

Figure 2. Scatter plot for best elk group habitat selection model variables, Jarbidge Mountains, Nevada, USA, 1998–2001. Predictor variables are distance (km) to nearest perennial stream from center of elk and random 2.3-km buffers and the ratio of aspen cover to conifer cover in each 2.3-km buffer. Data for 127 elk groups were averaged across 19 telemetry flights and are compared to data averaged for paired random buffers equal to the number of elk groups per flight.

Table 2. Fit statistics for the top 7 candidate models explaining cow elk group habitat selection in summer, Jarbidge Mountains, Nevada, USA, 1998–2001. Logistic regression modeling compared habitat use within 2.3-km buffers around 127 cow elk group locations averaged across 19 fixed-wing flights with averages for 19 equal groupings of 127 random 2.3-km buffers representing habitat availability. Groupings led to $n = 38$ observations evaluated for each model. Models are listed according to the model best fitting the data and ranked by (Δ_i), the difference between the model with the lowest Akaike's Information Criterion for small samples (AIC_c) and the AIC_c for the current model. The value of the maximized log-likelihood function (log[L]), the number of estimated parameters (K), and Akaike weights (w_i) for each model are also presented.

Model[a]	Log(L)	K	AIC_c	Δ_i	w_i
H2O + X2	−6.43	3	19.564	0.000	0.996
H2O + X4	−12.61	3	31.919	12.355	0.002
X2 + X4	−13.23	3	33.164	13.600	0.001
MAHOG + X2	−15.07	3	36.848	17.284	0.000
X2	−16.57	2	37.488	17.924	0.000
COOL + X2	−16.32	3	39.348	19.784	0.000
ROAD + X2	−16.48	3	39.658	20.094	0.000

[a]Abbreviations for habitat predictor variables are percentage of cool aspect (COOL) in each 2.3-km buffer, distance (km) from buffer center to the nearest perennial stream (H2O), percentage mahogany cover (MAHOG) in each buffer, distance (km) from buffer center to the nearest road (ROAD), ratio of aspen cover to conifer cover (X2) in each buffer, and ratio of sagebrush cover to snowbrush cover (X4) in each buffer.

Figure 3. Proportion of cover types within 6 probability classes of cow elk group habitat selection, Jarbidge Mountains, Nevada, USA, 1998–2001. Distribution of each cover type among probability of use classes was bimodal reflecting 1) the low probability of selection ($P \leq 0.10$) for cover occurring far from water and in areas with more conifer cover relative to aspen cover, and 2) the high probability of selection ($P \geq 0.95$) for cover close to water in areas with higher aspen cover relative to conifer cover.

fewer elk would use mahogany and snowbrush cover types than the original I_{NCC} models predicted. Probabilities of habitat selection in our study were highest in areas near perennial streams with high aspen cover and low conifer cover. Population objectives based solely on nutritional resources would invariably lead to overuse of aspen, conifer, and sagebrush–herb communities. The

protocol we developed to adjust nutritional carrying capacity estimates with patterns of habitat selection provides a critical refinement to nutritional carrying capacity models. It follows that traditional nutritional carrying capacity estimates have likely been biased toward a higher number of animals than if those estimates incorporated habitat-use patterns.

Nutritional carrying capacity estimates adjusted with RSFD may be generous considering that elk likely use portions of summer range in autumn for periods longer than the approximated lengths. Alteration of favored areas is likely to occur as ungulates reach densities approaching I_{NCC} estimates. By comparison, 30-year simulation models conducted by Weisberg et al. (2002) to evaluate effects of increasing levels of elk in a northern Colorado population indicated that decline in herbaceous root biomass was greatest in sagebrush grassland and aspen and least for conifer forest and irrigated hayland. It is not clear at what level ungulate populations may alter composition of forage bases in particular plant communities; however, it is clear that as ungulates reach carrying capacity, forage use will influence plant community composition (e.g., Irwin et al. 1994).

Residual SDE in our carrying capacity estimates reflects use by livestock and wildlife including elk. Herbivory from increasing elk populations in concert with stable populations of livestock and other wildlife will reduce the availability of SDE for elk by 1 September. However, constraints on SDE availability included in our I_{NCC} estimates afford surplus SDE in each community that is largely unused at low densities. This point further suggests that impacts to aspen and sagebrush–herb communities are most likely to occur as the population nears I_{NCC} and makes increasing use of forage in each community. In addition, the ability of plant communities to provide adequate nutrients for cow elk to achieve good performance will likely decrease as autumn forage abundance

Table 3. Summer range economic nutritional carrying capacity estimates (I_{NCC}) for 236-kg lactating cow elk in 5 cover types, Jarbidge Mountains, Nevada, USA, autumn 1999 and 2000. Estimates reflect nutritional levels for maintenance (2,550 kcal/kg) and good (2,750 kcal/kg) animal performance. Original I_{NCC} estimates for each cover type were adjusted when expected elk densities predicted with the resource selection function from the best logistic regression model (RSFD) exceeded original I_{NCC} estimates. Differences indicate the influence of predicted habitat selection on original estimates. Original I_{NCC} estimates were adjusted to avoid estimates that would promote overuse of forage in communities.

	1999			2000		
Performance	Original	RSFD[a]	Difference[b]	Original	RSFD[a]	Difference[b]
Maintenance						
Aspen	302	753	−451	239	492	−253
Conifer	74	35	39	19	23	−4
Mahogany	530	451	79	358	295	63
Sagebrush–herb	1,079	1,139	−60	698	744	−46
Snowbrush	548	153	395	341	100	241
Total[c]	2,533	2,531	−511	1,655	1,654	−303
Adjusted I_{NCC}	2,022			1,352		
Good						
Aspen	267	673	−406	164	327	−163
Conifer	20	31	−11	5	15	−10
Mahogany	468	403	65	332	196	136
Sagebrush–herb	1,001	1,018	−17	283	494	−211
Snowbrush	508	136	372	316	66	250
Total[c]	2,264	2,261	−434	1,100	1,098	−384
Adjusted I_{NCC}	1,830			716		

[a] Carrying capacity density estimates in each cover type redistributed with the resource selection function (RSFD).
[b] Differences are predicted RSFD estimates subtracted from original I_{NCC} estimates.
[c] Total I_{NCC} estimates redistributed with RSFD differ from original I_{NCC} estimates due to rounding error.

declines at higher elk densities. Because our carrying capacity estimates were based on constrained forage availability, this elk population will not be required to shift habitat selection to find more forage because predicted elk densities will ultimately be lower than levels that would consume all available forage in communities such as aspen and sagebrush. We would expect greater use of conifer, mahogany, and snowbrush cover types and areas further from perennial streams as elk increase in numbers. However, impacts on aspen and sagebrush–herb communities will likely increase even in the face of shifting habitat-selection patterns. A reanalysis of habitat and forage selection patterns as this population nears I_{NCC} would clarify these relationships and provide a validation of our habitat model.

Weather conditions in 2000 reflected an average snowpack water year followed by a warmer summer with less than 50% of the precipitation than in 1999, another normal snowpack year. Length of autumn 2000 was maximum at 76 days; thus, adjusted maintenance performance estimates using 2000 data provide a reasonable approximation of carrying capacity for long, dry autumns when forage production and nutrients are limited. Population objectives based on estimates in years with limited resources will ensure provision of ample nutritious resources during lean periods to elk population levels that should not appreciably alter vegetation conditions.

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. 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- to 2,347-m elevation (modal elevation = 2,070 m), typically in moist sites or where snow accumulates (Mueggler 1988). Snowbrush grew adjacent to or in aspen in snowbank associations throughout the study area. Furthermore, spectral reflectance for snowbrush and aspen was similar; consequently, the high level of elk selection we detected for snowbrush (although it only comprised 3% of the area above 2,135 m) was likely related to association with aspen (Rettie and McLoughlin 1999).

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 were 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 road densities will reduce habitat effectiveness for elk.

Management Implications

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 at maintenance levels 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).

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 whether elk populations will exhibit density-dependent responses such as lower calf survival, declining population growth, and reduced antler and body sizes as they reach 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 that ungulate populations are most productive when they are maintained at species-specific levels far below K_{CC} (Wisdom and Cook 2000, McCullough 2001). It is clear that maintaining elk populations at or below adjusted I_{NCC} levels will assist in maintaining population productivity while not overly jeopardizing the vegetation resources that sustain elk and other ungulates on shared ranges.

Acknowledgments

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Appendix A. Standing digestible energy (SDE) available (kcal/ha), SDE intake (kcal/ha), and % of total SDE intake by forage species included in economic nutritional carrying capacity models at maintenance (2,550 kcal/kg) and good (2,750 kcal/kg) performance levels for lactating cow elk in autumn, Jarbidge Mountains, Nevada, USA, 1999 and 2000. Blanks (–) indicate models in which SDE was too low to incorporate as intake following application of Hobbs and Swift's (1985) algorithm. Availability and intake of SDE represent values across approximated lengths of autumn (1999 = 53 days; 2000 = 76 days). Standing digestible energy available in forbs and graminoids was based on perennial forbs and perennial graminoids.

| | 1999 | | | | | | 2000 | | | | |
| | | Maintenance | | Good | | | | Maintenance | | Good | |
Cover type	SDE available kcal/ha	Intake kcal/ha	Intake %	Intake kcal/ha	Intake %	SDE available kcal/ha	Intake kcal/ha	Intake %	Intake kcal/ha	Intake %
Aspen										
Aspen	9.60×10^3	2.59×10^1	0.2	2.81×10^1	0.2	3.92×10^4	1.15×10^2	1.0	1.15×10^2	1.3
Forbs	2.17×10^5	1.31×10^3	11.2	1.35×10^3	11.1	2.32×10^5	1.53×10^3	12.8	1.07×10^3	12.6
Graminoids	1.74×10^5	–	–	–	–	2.82×10^5	–	–	–	–
Snowberry	1.95×10^4	5.25×10^1	0.4	5.70×10^1	0.5	2.74×10^4	8.02×10^1	0.7	8.02×10^1	0.9
Conifer										
Forbs	7.79×10^4	3.34×10^2	2.9	1.01×10^2	0.8	7.20×10^4	1.26×10^2	1.1	2.99×10^1	0.4
Graminoids	5.09×10^4	–	–	–	–	4.80×10^4	–	–	–	–
Snowberry	3.35×10^3	6.41×10^0	0.1	6.96×10^0	0.1	3.21×10^3	6.67×10^0	0.1	6.67×10^0	0.1
Mahogany										
Forbs	1.91×10^5	1.52×10^3	13.0	1.64×10^3	13.4	1.84×10^5	1.58×10^3	13.3	1.58×10^3	18.6
Graminoids	1.64×10^5	1.15×10^2	1.0	–	–	1.97×10^5	–	–	–	–
Mahogany	2.53×10^4	8.91×10^1	0.8	9.67×10^1	0.8	1.82×10^5	6.98×10^2	5.9	6.98×10^2	8.2
Snowberry	2.06×10^5	7.28×10^2	6.2	7.90×10^2	6.5	7.69×10^4	2.94×10^2	2.5	2.94×10^2	3.5
Sagebrush										
Forbs	2.48×10^5	4.64×10^3	39.7	5.04×10^3	41.2	2.30×10^5	4.66×10^3	39.2	1.84×10^3	21.6
Graminoids	2.17×10^5	–	–	–	–	1.88×10^5	–	–	–	–
Snowberry	4.70×10^4	3.38×10^2	2.9	3.67×10^2	3.0	4.51×10^4	3.52×10^2	3.0	3.52×10^2	4.1
Snowbrush										
Snowbrush	5.31×10^6	2.53×10^3	21.6	2.75×10^3	22.5	4.73×10^6	2.45×10^3	20.6	2.45×10^3	28.7