Modeling Nutritional Carrying Capacity for Translocated Desert Bighorn Sheep in Western Texas

Randall W. DeYoung\(^1,4\)  
Eric C. Hellgren\(^2,5\)  
Tim E. Fulbright\(^1\)  
W. Frank Robbins, Jr.\(^1\)  
Ira D. Humphreys\(^3\)

Abstract

Restoration of desert bighorn sheep (Ovis canadensis) is proceeding in several western states. Measurement of nutritional resources (quality and quantity) is not normally conducted to assess future and present translocation sites, although it has been recommended generally for evaluation of ungulate habitat. We estimated nutritional carrying capacity (based on nitrogen in forage species) of three mountain ranges in Trans-Pecos Texas where desert bighorn sheep have been translocated. We used an explicit nutritional constraint model to estimate carrying capacity on a seasonal basis. Although drought conditions prevailed during the study period, bighorns were not limited by quantity of vegetation. However, forage biomass of high nutritional quality (>1.5% N) was very low (<9 kg/ha in spring; <1 kg/ha in all other seasons). Consequently, there appeared to be inadequate forage of high N content for bighorns to meet reproductive requirements in some seasons. Estimates generated using the explicit nutritional constraint carrying capacity model appeared to be realistic relative to observed densities. Nutritional sampling and modeling can predict potential carrying capacity on areas scheduled for restoration or on ranges already stocked, predict effects of management on carrying capacity, and allow managers to compare among restoration sites. We recommend that desert bighorn managers focus on monitoring the abundance of high-quality (%N) forage species, especially during periods of drought or higher nutritional requirements (e.g., lactation, post-weaning growth).

Key words: bighorn sheep, carrying capacity, desert, forage quality, habitat, nutrition, Ovis canadensis.

Desert races of bighorn sheep (Ovis canadensis cremnobates, O. c. mexicana, O. c. nesloni, O. c. weemsi) have declined since the arrival of Europeans to North America, and this decline has been precipitous since 1900 (Buechner 1960; Krausman & Shackelton 1999). Causes implicated in this decline include disease, competition from domestic livestock and feral ungulates, and human disturbance. The nominate race Ovis c. mexicana historically inhabited many of the mountain ranges in western Texas at the southeastern edge of the geographic range of desert bighorn sheep. Like desert bighorns elsewhere, Texas bighorns declined sharply after 1900 (Davis & Taylor 1939; Schmidly 1977; Monson & Sumner 1980). Bailey (1905) estimated 16 Texas mountain ranges supported bighorns. Three decades later, Davis and Taylor (1939) reported recent bighorn sightings in only 11 mountain ranges, and described Texas bighorns as threatened with extinction. They estimated that the bulk of the population (ca. 300) occurred in four areas: the Beach, Baylor, Carrizo, and Sierra Diablo Mountains. The population declined to about 150 in the 1940s, and became extinct in the 1960s (Monson & Sumner 1980). The last recorded sighting of a native Texas bighorn was reported by the Texas Parks and Wildlife Department (TPWD) in the Sierra Diablo Mountains in 1960 (Schmidly 1977).

Restoration of desert bighorn sheep in Texas began in 1957 when the TPWD determined that native bighorns were close to extinction. Presently, about 100 captive and 300 free-ranging bighorns occur in Texas in at least 5 populations or metapopulations (Altman 1999). They were restocked into previously occupied habitat, which was assumed suitable.

Vegetation change induced by overgrazing or shrub invasion (Risenhoover & Bailey 1985; Etchberger et al. 1995).
Bighorn Sheep Carrying Capacity

1989) can make previously occupied range unsuitable from the standpoint of forage quality and quantity. Indeed, forage production and quality are factors in regulating bighorn populations (Stelfox 1976), and may influence growth, reproduction, and behavior (Geist 1971). However, desert bighorn habitat models routinely do not use estimates of nutritional resources as criteria to assess foraging areas (McCarty & Bailey 1994). Current habitat suitability estimates used to evaluate potential restocking sites in Texas do not consider quality or quantity of vegetation, whereas vegetation composition is established through an ocular estimate (G. Calkins, TPWD, personal communication). Better quantification is desirable.

Estimates of carrying capacity on a nutritional basis have been recommended for habitat evaluation, especially for habitat comparison (Hobbs et al. 1982). Carrying capacity is often determined for wintering ungulates under the assumption that forage is limiting in the winter (Hobbs et al. 1982; Potvin & Huot 1983). However, yearly fluctuation in forage availability and nutrient content due to variable precipitation is probably the greatest factor influencing desert ungulate populations (Wehausen et al. 1987). In addition, nutritional carrying capacity is constantly fluctuating among seasons, and estimates are merely approximate averages of the fluctuations.

Desert environments are, by definition, areas of low primary production and cannot support high populations of large-bodied herbivores. Therefore, models that estimate carrying capacity can be particularly important in the conservation, restoration, and management of desert bighorn sheep. Models can predict potential carrying capacity on areas scheduled to receive translocations of bighorns, predict carrying capacity on ranges already stocked, predict effects that changes in variables have on carrying capacity, and allow managers to evaluate habitat. Previous estimates of nutritional carrying capacity, using traditional models (e.g., Hobbs et al. 1982) have concluded that forage was not a limiting factor for bighorns (Mazaika et al. 1992). However, these estimates, which calculated carrying capacity based on total range supply of nutrients divided by animal demand, included forage of submaintenance quality and were not capable of detecting interactions between carrying capacity and the animal’s nutritional state (Hobbs & Swift 1985). Model incorporation of forage biomass of insufficient quality to support maintenance requirements biases estimates upward.

Our objectives were to estimate nutritional carrying capacity (based on % N in forage plants) of desert bighorn habitat in three mountain ranges where bighorns have been restored, to compare these estimates to observed densities of bighorns, and to evaluate the utility of nutritional assessments of bighorn habitat. To accomplish these objectives, we used an explicit nutritional constraint model (Hobbs & Swift 1985) that integrates measures of forage quality and quantity.

Study Area

Carrying capacity was determined on three study areas, one in each of the Baylor and Beach Mountains in Culberson county, and one in a portion of the Sierra Diablo Mountains in Hudspeth and Culberson counties known as Victorio Canyon (part of the Sierra Diablo Wildlife Management Area). The Baylor (31°15’ N, 104°47’ W), Beach (31°7’ N, 104°5’ W), and Sierra Diablo (Victorio Canyon 31°2’ N, 104°6’ W) Mountains lie in a north–south orientation, and encompass about 84, 46, and 12 km² (Victorio), respectively (Fig. 1). They are located 170 km east of El Paso, and 7 km north of Van Horn, Texas. Elevations range from 1,360 to 1,960 m, and the terrain varies from desert flats to rugged canyons and cliffs with rolling tops. The long-term average annual precipitation is 32.5 cm (NOAA 1995), but the area received considerably less in our study period (1993: 16.1 cm; 1994: 17.2 cm; 1995: 25.3 cm; NOAA 1992–1995).

Warnock (1974) described the vegetation of the Baylor and Beach Mountains as a chino grama (Bouteloua ramosa)–lechuguilla (Agave lechuguilla) association, and that of the Sierra Diablo Mountains as grassland with dense stands of pinon pine (Pinus cembroides), Pinchot juniper (Juniperus pinchotii), and oak (Quercus spp.). Other important plants in these associations include Mormon tea (Ephedra spp.), sotol (Dasylirion spp.), ocotillo (Foquera splendens), and prickly pear (Opuntia spp.) (Schmidly 1977). Common grasses include grama grasses (Bouteloua spp.), threeawns (Aristida spp.), muhlys (Muhlenbergia spp.), needlegrasses (Stipa spp.), and dropseeds (Sporobolus spp.) (Gould 1974; Hatch et al. 1990).

Figure 1. Location of Baylor, Beach, and Sierra Diablo Mountain study areas in western Texas near Interstate Highway 10 (I-10).
All areas have been historically grazed by cattle, and some by domestic sheep and goats. During the study, portions of all areas were grazed by cattle and a few groups of domestic horses, but livestock use was usually limited to the flats and canyon bottoms away from bighorn populations. Ranch roads facilitated access to portions of the Baylor and Beach Mountains, while the Victorio Canyon area was only accessible by foot beyond the entrance to the Sierra Diablo Wildlife Management Area (WMA).

**Methods**

**Population Trends**

Bighorn sheep in the study areas were considered a metapopulation by TPWD due to sheep movements among the ranges. Desert bighorns were restored to the Sierra Diablo in 1973, the Baylor Mountains in 1988, and the Beach Mountains in 1991. The bulk of this metapopulation occurs on private land and the TPWD cannot always obtain access to survey the same areas each year. However, sheep habitat in the Baylor and Beach Mountains was readily accessed by the TPWD. Bighorn sheep were counted by helicopter surveys each fall. Data were collected on herd composition (males, females, lambs) and total number of sheep (Altman 1999).

**Diet Composition**

We collected fresh fecal samples (<6 hr) seasonally during 1994–1995 from bighorns in the study areas. Bighorns were visually located with binoculars and a spotting scope. Fecal samples were collected only from observed defecation where the subjects were positively identified to sex. We attempted to collect more than 20 fecal groups (>10 fecal pellets in a 25 cm radius) seasonally per sex in each area (season–area–sex combination) for 2 years. Feces were placed in sterile plastic bags, stored on ice to inhibit microbial action, and frozen within 24 hours. Samples were freeze-dried and ground in a Wiley mill through a 1 mm mesh screen. A 1 g subsample was taken from each fecal sample. Subsamples from each season–area–sex combination were composited and sent to the University of Arizona for microhistological analysis. Compositing of fecal samples has been found to be efficient, cost-effective, and accurate (Jenks et al. 1989).

**Seasonal Forage Production**

We randomly selected four vegetation sampling sites within bighorn habitat (as determined by observation and fecal collection) in each study area. We divided each site into three elevation classes: upper (including tops of ridges and peaks), middle, and lower slopes (not including canyon bottoms or flats because these areas received little use). At each site, we established permanent 100 m transects in a stratified, random manner. Five transects per elevation class were sampled during spring, but three transects per elevation class were sampled in all other seasons due to time constraints.

In 1995, we estimated seasonal biomass of forage species using a double-sampling technique (Bonham 1989). Sampling occurred in March, June, September, and December. Plots measuring 0.5 m² by 1.5 m high (0.75 m³) were placed at 10 m intervals along each transect. Plant species that composed >1% of bighorn diets in 1994 were considered forage species. Forage species within each plot were clipped at a 3:10 ratio (3 plots clipped for every 10 plots sampled) during spring, and at a 4:10 ratio in all other seasons (clipping intensity was increased to partially offset the reduction in the number of transects). Sample size was determined to be adequate using species-area curves and running means (Bonham 1989). Individual plots were not sampled more than once. We sampled 600 plots per area in spring, and 360 plots per area in other seasons. The reduction in sampling occurred because of the logistical difficulty in sampling 5 transects per elevation class per site per mountain range in a period within each season short enough to allow for other work (e.g., animal observation) to continue. Clipped forages were separated by species and weighed (wet weight) in the field. Clipped samples were later air-dried at room temperature and reweighed. Subsamples were oven-dried at 105°C for 24 hours to determine dry mass (DM).

Wet weights of forage species were converted to DM using a ratio estimator of wet:dry matter for each species in each season–area combination. Forage species that were estimated but not clipped were converted to DM using a wet:dry matter ratio by forage class (i.e. browse, forbs, grass, succulents) for each area in each season. Biomass of plant species present in bighorn diets, but not encountered during vegetation sampling, was entered into carrying capacity calculations as a minimum value. The minimum value was estimated by assuming each plant species that appeared in the diet was at least as abundant as the forage species encountered during vegetation sampling periods that had the least measurable biomass (6 g/ha) on a DM basis.

**Chemical Composition of Forages**

In 1995, we hand-plucked samples of forage species composing more than 1% of 1994 bighorn diets. We assumed that we collected plant parts that bighorns would select, such as current-year’s growth of browse and grass, and leaves and green stems of forb species. Hand-plucked samples were air-dried at room temper-
ature to constant mass. Subsamples of hand-plucked species were oven-dried at 105°C for 24 hours to determine DM. Forage samples were ground through a Wiley mill with a 1 mm mesh screen and stored in sealed sterile plastic bags. We analyzed forage samples for %N with a PE2410 Series II Nitrogen Analyzer (Perkin Elmer, Norwalk, Connecticut, USA). If a species occurred in the diet, but was not encountered during vegetation sampling in a given study area, nutritional value of the same species from another study area during the same season was substituted. Percent N from plant species present in the diet but not encountered in the study areas in 1995 were taken from literature values (DeYoung 1997).

Carrying Capacity

We defined carrying capacity as the number of animals at specific nutrient requirement levels that a given habitat can support during a season. We used the explicit nutritional constraint model, developed by Hobbs and Swift (1985), to estimate seasonal carrying capacity for bighorns. This model assumes (1) that ungulates will select higher-quality forage items in preference to lower-quality forage items; and (2) that the forage species and plant parts upon which the estimates will be based account for distinctions ungulates make among forage plant parts (e.g., stems vs. leaves) if these parts differ in nutritional quality. It requires data on biomass and nutrient concentration of forage. We estimated nitrogen-based carrying capacity (Hobbs & Swift 1985), although a modification of the model allows simultaneous consideration of digestible dry matter (as a surrogate for digestible energy) and digestible protein (Hanley & Rogers 1989). We did not have estimates of digestible dry matter or energy for all available forage species to fully parameterize the model. Hobbs and Swift (1985) did not estimate variance or provide confidence limits for their model outputs.

We estimated carrying capacity for each season of vegetation sampling. The number of bighorns/km² were calculated on the basis of an average 75 kg bighorn sheep (Hebert 1973). We defined available forage as 50% of that present under the assumption that more than 50% use may result in habitat deterioration (Wallmo et al. 1977). Nutrient content of forages was determined as described above. Each season was 90 days in length. Forage items that composed more than 1% of bighorn diets in 1994 or 1995 (as determined by microhistological analysis) were used in carrying capacity estimates.

The least amount of biomass that we estimated for an individual plant species was 6 g/ha. We rarely or never encountered many preferred forbs. Recent research on plant sampling in desert habitats suggests that many sampling methods do not generate good estimates of abundant species; rare species are often overlooked or poorly estimated (Etchberger & Krausman 1997). We assumed that a plant species must occur at ≥6 g/ha to appear in the diet, and used this value as the minimum biomass for plant species present in the diet but not encountered during vegetation sampling.

Nutritional Requirements

We assumed daily intake (1.9 kg DM/day) and N maintenance requirements (17 g N/day = endogenous urinary N + metabolic fecal N) for an average adult 75 kg bighorn, based on Hebert (1973). Lactation requirements for domestic ewes suckling single lambs are 1.5–1.7% N, while growth requirements for weaned domestic lambs are 1.8% N (Church & Pond 1982). We assumed that desert bighorns would require similar levels of N during lactation and post-weaning. Domestic sheep are the most closely related species to desert bighorns for which reproductive and growth requirements have been derived. We calculated carrying capacity using the explicit nutritional constraint model for bighorns consuming diets containing the following target concentrations of nitrogen: 0.89 (maintenance), 1.2 (above-maintenance), 1.5 (estimated lower limit for lactation), and 1.8% N (estimated growth requirement for lambs).

Results

Population Trends

Total sheep counted in the three-area metapopulation were 112, 122, 170, 160, 160, 132, and 160 from 1992 to 1998, inclusive (Altman 1999). Although overall numbers appeared stationary during our 1994–1996 study period (170–160–160), there was a distributional shift in sheep between the Baylor and Beach Mountains. Observed sheep increased in the Baylor Mountains from six in 1993 to 22 in 1994, 32 in 1995, and 25 in 1996. Concomitantly, the number of sheep observed in the Beach Mountains varied from 58 in 1993 to 88 in 1994, then dropped to 70 in 1995 and 59 in 1996. Numbers counted in the Sierra Diablo area were 58, 73, 58, and 76 from 1993 to 1996.

Diet Composition

Microhistological analyses of 411 bighorn pellet groups identified 35 plant genera used during the study period including 14 woody/shrub, 12 forb, and 9 grass genera (DeYoung 1997). The most common genera identified were, in order of abundance, wild buckwheat (Eriogonum spp.), globemallow (Sphaeralcea spp.), sagebrush (Artemisia spp.), Bouteloua spp. prickly pear, sumac (Rhus spp.), honey mesquite (Prosopis glandulosa), rat-
any (Krameria spp.), cloak fern (Notholeana spp.), and true mountain mahogany (Cercocarpus montanus). Plants of high nutritional value (>1.5% N in >1 season) found in the diet included globemallow, ratany, field ragweed (Ambrosia confertifolia), slender janusia (Janusia gracilis), sagebrush, dalea (Dalea spp.), filaree (Erodium spp.), Apache plume (Fallugia paradoxa), sumac, wild buckwheat, acacia (Acacia spp.), lupine (Lupinus spp.), Heath cliffrose (Cowania ericifolia), fleabane (Erigeron spp.), milkvetch (Astragalus spp.), and deervetch (Lotus oroboides).

### Seasonal Biomass Production

Prickly pear cladophylls, grama grasses, Mormon tea (Ephedra spp.), and muhly grasses (Muhlenbergia spp.) composed the majority of available forage in all seasons (DeYoung 1997). Browse (including prickly pear) was the most abundant forage class. Browse biomass showed no clear seasonal trends. Grasses, especially grama grasses (sideoats grama, B. curtipendula; black grama, B. eripoda; blue grama, B. gracilis; hairy grama, B. hirsuta) constituted a large amount of the available forage. The amount of grass available for consumption showed a general decline from spring through winter. Forb biomass was consistently low in all areas (Table 1), with many species present only in trace (<1 kg/ha) amounts. Spring was the only season when a diversity of forb species was found. Forb biomass declined from spring to summer, and only trace amounts were available in the study areas in fall and winter. Wild onion (Allium spp.) and wild buckwheat were the most common forb species.

### Carrying Capacity

Seasonal carrying capacity was lowest in autumn and winter and highest in spring. Carrying capacity estimates derived using the explicit nutritional constraint model varied greatly depending on the target concentration of N in the diet (Table 2). As target N increased above maintenance (0.89%), estimated carrying capacity declined precipitously to near zero in some seasons at the highest target concentration of N. In other words, fewer animals could be supported at a high nutritional plane because of a decreasing amount of forage of higher N levels. Estimated carrying capacity also decreased from spring and summer to fall and winter. There was very little biomass greater than 1.5% N after spring, but biomass of lower quality was abundant through summer. During fall and winter, large amounts of browse and grass were available (Table 1), but the low N content of this biomass limited the amount of browse and grass that could be consumed and still maintain target levels of dietary N (Table 2).

Estimated densities in the study area were 4.8–6.1, 0.3–0.4, and 1.5–1.9 bighorns/km² based on total sheep observed in the Sierra Diablo, Baylor, and Beach Mountains, respectively, in fall 1994 and 1995. Forage supplies for maintenance were not limiting at these densities for sheep in these ranges (Table 2). There was

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**Table 1.** Biomass (kg/ha dry matter) and mean (weighted average) percent nitrogen(N) of forage classes (includes only species composing >1% of bighorn diets) used by desert bighorn sheep in the Baylor, Beach, and Sierra Diablo (Victorio Canyon) Mountains, Texas, 1995. Variance of biomass estimates is based on 4 sites/mountain range, where each site was sampled with 9 100-m transects at an intensity of 10, 1-m² frames/transect.

<table>
<thead>
<tr>
<th>Season</th>
<th>Area</th>
<th>Forbs Biomass</th>
<th>Grasses Biomass</th>
<th>Browse Biomass</th>
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<tr>
<td></td>
<td></td>
<td>N</td>
<td>x</td>
<td>SE</td>
</tr>
<tr>
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<td>1.26</td>
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a Literature values used when species appeared in the diet but were not encountered during vegetation sampling.
b Opuntia spp. accounted for >77% of browse biomass in all seasons.
adequate high-quality forage in spring to meet lactation requirements in the Baylor and Victorio Canyon study areas, but the amount of high-quality forage in the Beach Mountains during this time produced diets marginal for lactation. In spring 1995, the Beach Mountains compared well with the other areas in forage biomass of maintenance quality, but had less forage biomass of higher quality (Table 2). However, by winter 1995, even the forage biomass available to support bighorns at maintenance (0.89% N) was greatly reduced (Table 2). In addition, there was inadequate forage to meet requirements of ewes lactating during summer in all areas. Averaging across seasons, the low-density population in the Baylor Mountains was not N-limited, but the high-density populations in Victorio Canyon and the Beach Mountains were limited at higher concentrations of diet N (≥1.5%) associated with lactation and post-weaning growth.

Discussion

Our data suggest that bighorns were not limited by overall quantity of forage. However, there was very little forage of high quality, which reduced total usable biomass to a fraction of the total available biomass. Diet quality (N) of desert bighorns in our study areas was at or below required levels of N during much of 1994–1995 (DeYoung 1997). There was enough high-N forage to support only low densities of bighorns and meet their maintenance (0.89% N) and lactational (1.5% N) requirements in some seasons (Table 2). Forage of sufficient quality to meet the demands of late lactation and post-weaning growth of lambs in summer and early fall was in short supply, especially in the high-density Beach population. These results exemplify the contention of Hobbs and Swift (1985) of the density-dependent nature of animal–food interactions. As animal numbers increase, the quality of diet obtainable declines.

How do these modeling results relate to observations on the bighorn sheep population? Juxtaposition of carrying capacity estimates with survey data show some interesting affinities. For example, the Beach Mountains are a relatively small mountain range, yet supported the greatest number of observed bighorns of the three areas. The decrease in carrying capacity from spring to winter 1995 relative to extant sheep densities suggests that overuse of the habitat may have occurred during this time. The increased sheep observations in the Baylor Mountains coincident with declines in the Beach Mountains in fall 1995 were consistent with sheep moving from an area of low carrying capacity to an area of higher carrying capacity (Table 2). In addition, the rapid growth of the sheep populations in the early 1990s slowed, then reversed by 1997. These changes are consistent with our carrying capacity modeling. We hypothesize that recruitment of lambs during the study period was reduced because of drought-induced nutritional limitation. The proximate cause behind this reduction was inadequate forage quality in available biomass to support growth of weaned lambs through fall and winter, especially in the Beach Mountains. Unfortunately, identification of yearlings in helicopter surveys is problematic (Bleich 1998), so we cannot assess our hypothesis.

Biomass of forages in desert bighorn sheep habitats is poorly documented. Consumable biomass of forage species in our study areas, especially forbs, was lower (233–676 kg/ha) than reported by Mazaika et al. (1992) in the Pusch Ridge Wilderness in Arizona (seasonal range 851–1,985 kg/ha). Forb biomass reported by Mazaika et al. (1992) ranged from 429 kg/ha in spring to 211 kg/ha in winter. Drought conditions during 1993–1995 probably explain the low forb biomass and rarity of forbs and other forage species in our areas. However, forage production in our study areas was greater than the 33–73 kg/ha reported for desert bighorn habitat in Canyonlands National Park, Utah (Bates & Workman 1983). In previous studies, carrying capacity estimates were gross overestimates of true population carrying capacity because forage of submaintenance quality was in-

<table>
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</table>

Table 2. Seasonal nutritional carrying capacity estimates (in animals/km²) in 1995 for desert bighorn sheep in the Baylor, Beach, and Sierra Diablo (Victorio Canyon) Mountains, Texas, derived using the explicit nutritional constraint model (Hobbs & Swift 1985), based on the amount of nitrogen in bighorn forage species. Numbers represent estimated number of animals/km² that can be supported at maintenance (0.89%), above-maintenance (1.2%), lactation (1.5%), or growth (1.8%) requirements of nitrogen.
cluded in estimation. In range-supply models (Hobbs et al. 1982; Svejcar & Vavra 1985), a significant portion of the available biomass used to calculate these carrying capacity estimates is not available because it is of insufficient quality to support animal maintenance requirements. For example, Mazaika et al. (1992) estimated the carrying capacity of desert bighorn habitat in the Pusch Ridge Wilderness, Arizona, to be 160–300 adult bighorns/km², a value that greatly exceeded population estimates (2–4 animals/km²). These authors reasoned that bighorn populations did not approach carrying capacity because resources were also available to sympatric ungulates, which were not accounted for in the model. This may be partly true, but high carrying capacity estimates also were generated from inclusion of submaintenance forage (especially grasses; mean N = 0.64%) in measures of available forage. Also, previous estimates may be biased because of apparent miscalculations. Estimates of estimated carrying capacity of Rocky Mountain bighorns on winter range in Canada (50–180 bighorns/km²) by Stelfox (1976) require reevaluation because he approximated daily forage intake as 1 kg DM/day. Goodson et al. (1991) observed Rocky Mountain bighorn daily intake rates of 0.9–2.4 kg/day, while Hebert (1973) estimated Rocky Mountain bighorn intake at 1.9 kg DM/day. Mazaika et al. (1992) reported daily intake rates of 2.7–4.2 kg/day for two captive adult desert bighorn rams on native forage.

Estimated carrying capacities for diets above maintenance that were generated using the explicit nutritional constraint model were similar to observed densities of desert bighorns on our study areas and in other states. Observed densities of desert bighorns include 0.1 bighorns/km² in western Arizona (Krausman et al. 1989), 0.6 bighorns/km² in the Mojave desert of California (Bleich 1993), 2.3–3.1 bighorns/km² in the River Mountains of Nevada (Leslie & Douglas 1979), and 2–4 bighorns/km² in the Pusch Ridge Wilderness of Arizona (Mazaika et al. 1992). Although our density estimates (0.3–6.1 animals/km²) are based on uncorrected sighting data, published mean sighting probabilities for bighorns range from 0.58 to 0.67 (Neal et al. 1993; Bodie et al. 1995). Correcting our data for visibility bias increases density estimates by 50–75% and strengthens our comments about nutritional limitation.

Several factors may influence carrying capacity and its estimation. Bighorn habitat use varies seasonally (Gionfriddo & Krausman 1986; Fairbanks et al. 1987) and may influence carrying capacity. Differences in resource use between sexes also influence carrying capacity. Sexual segregation and differential habitat use have been documented in bighorns (Geist & Petocz 1977; Shank 1982; Gionfriddo & Krausman 1986). Several explanations have been developed to explain sexual segregation and possible advantages of sexual segregation in ungulates (Main & Coblentz 1990). Many carrying capacity estimates, including ours, are based on an animal unit or an average adult male. If differences in diet between sexes are large and sexes segregate throughout most of the year, the sex ratio of the population may influence carrying capacity. Carrying capacity for a female-biased population would be higher because female bighorns are smaller in mass than males and have smaller absolute nutritional requirements.

A related factor affecting our estimates may have been assumptions regarding body mass and daily intake rates. For example, if the average adult body mass in our study areas was less than 75 kg, intake would be less than we assumed and our modeled estimates of carrying capacity would be negatively biased. Body mass of desert bighorn sheep in Nevada averaged 71 kg for adult males and 44 kg for adult females (Aldous et al. 1958), for an average of 57 kg, or 24% less than 75 kg. Given this level of bias, our conclusions remain unchanged, however.

Changes in food supply and availability may result in diet overlap between sympatric ungulates, and, potentially, competition (Spowart & Hobbs 1985). Competition for forage resources between herbivores may have the greatest effect on carrying capacity if diet overlap between species is high and forage is limiting. Introduction of livestock and exotic and feral ungulates has led to competition being implicated in the decline of bighorns in former ranges (Hansen 1982). Mule deer are not thought to compete for resources directly with bighorns; these species have coexisted in desert environments for many years (Bailey 1980). Mule deer diets contain primarily browse while Rocky Mountain bighorn diets contain primarily grasses. Krausman et al. (1989) found no significant dietary overlap between desert bighorns and mule deer. As a result, researchers have concluded that because of the low diet overlap, competition did not exist (Hobbs et al. 1983; Spowart & Hobbs 1985). However, shrubs often compose more than 50% of desert bighorn diets (Rominger et al. 1988; Krausman et al. 1989; Miller & Gaud 1989; Mazaika et al. 1992; present study). Also, in some situations, such as on burned range, diet overlap between bighorns and mule deer increases (Spowart & Hobbs 1985). Therefore, the potential for competition exists in areas where desert bighorns and mule deer share similar habitat, and should be considered when estimating carrying capacity (Campbell & Johnson 1983).

We conclude that our estimation of carrying capacity had practical value in measuring the ability of a habitat to support animals under specified conditions (Hanley & Rogers 1989). The explicit nutritional constraint model (Hobbs & Swift 1985) derived estimates of carrying capacity that compared well with observed densities of desert bighorns, and can be used with data collected for use in traditional carrying capacity models. We propose
that such models can predict potential carrying capacity on areas scheduled for restoration or on ranges already stocked, predict effects that changes in variables have on carrying capacity, and allow managers to compare among restocking sites. The labor-intensive sampling used to derive these estimates is a drawback to this method. We recommend that sampling occur during the period most likely to be nutritionally limiting. Sampling during prolonged drought may be particularly informative by providing a minimal estimate.

We recommend those involved in conservation and restoration of desert bighorn sheep use key-plant principles (Holechek et al. 1989) to assess population translocation sites and to monitor trends in habitat after an introduction. Abundance of key forage species of high nutritional quality (Krausman et al. 1989) should be measured before restoration and monitored after restoration to gauge utilization, especially during prolonged drought conditions or critical nutritional periods such as late gestation, lactation, and post-weaning of lambs.

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