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Author(s): N. T. Hobbs, D. L. Baker, J. E. Ellis, D. M. Swift and R. A. Green
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ENERGY- AND NITROGEN-BASED ESTIMATES OF ELK WINTER-RANGE CARRYING CAPACITY

N. T. HOBBS,[1] Natural Resource Ecology Laboratory and Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523
D. L. BAKER, Colorado Division of Wildlife, Wildlife Research Center, 317 West Prospect, Fort Collins, CO 80526
J. E. ELLIS, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523
D. M. SWIFT, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523
R. A. GREEN, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523

Abstract: Carrying capacity of winter range for elk (Cervus elaphus nelsoni) was estimated based on range supply of energy and nitrogen during 1976–78 in Rocky Mountain National Park. Based on energy requirements of a 200-kg elk, winter-range carrying capacity was 1,481 ± 261 animals during Year 1 and 991 ± 102 during Year 2. Nitrogen-based estimates were similar to energy-based predictions: 1,674 ± 270 elk (Year 1) and 994 ± 101 (Year 2). Individual habitat types differed in carrying capacity. Willow (Salix spp.), wet meadow, and wet shrub meadow could support the most elk; aspen (Populus sp.) and mesic meadow were intermediate in carrying capacity; and sagebrush (Artemisia spp.), grassland, and ponderosa pine (Pinus ponderosa)-shrub could carry the fewest animals. Sensitivity analysis showed predictions of the range supply–animal demand model of nutritional carrying capacity to be strongly influenced by small changes in elk metabolic fecal nitrogen excretion rates. We conclude that the temporal variation in carrying capacity is important in managing harvest of elk populations and in planning future carrying-capacity research, and that estimates of nutritional carrying capacity are viable habitat evaluation procedures, particularly when used for comparative purposes.

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How many animals can make a living in a given ecosystem? The seemingly simple question of carrying capacity, often misunderstood, is fundamentally important to management of wildlife populations and the habitats they occupy (Caughley 1976, 1979). Recently, much interest has focused on procedures for estimating supportable population density of wild ungulates based on range supply of nutrients, primarily energy and nitrogen, and individual animal nutrient requirements. Algorithms for estimating carrying capacity have been developed, and prolific research has been conducted to provide data necessary for implementation of these models (reviewed by Moen 1973, Robbins 1973, Mautz 1978). Despite these efforts, the nutritional ap-proach to carrying capacity has been infrequently used to evaluate the quality of ungulate habitat (Bobeck 1977, Wallmo et al. 1977).

We estimated carrying capacity of winter range for elk during 1976–78 in Rocky Mountain National Park, Colorado, based on quantification of forage energy and nitrogen supply and extant knowledge of elk energy and nitrogen requirements. The objectives of this paper are to demonstrate that estimates of nutritional carrying capacity are viable habitat-evaluation procedures and to identify sensitive parameters in the range supply–animal demand algorithm.

[1] Present address: Colorado Division of Wildlife, Wildlife Research Center, 317 West Prospect, Fort Collins, CO 80526.

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STUDY AREAS AND METHODS

Investigations were conducted on upper montane (Marr 1967) winter range within Rocky Mountain National Park on the east slope of the Continental Divide between 2,500 and 2,800 m in elevation and 8 km west of the town of Estes Park, Colorado. Total area of this winter range is about 4,000 ha, 2,000 of which provide substantial amounts of forage. Eight habitat types are used by elk for feeding. A detailed description of these communities, as well as weather conditions and topography of the winter range, was given by Hobbs et al. (1981).

Carrying-capacity Model

Carrying capacity for the winter range was calculated according to a modification of the formula of Mautz (1978):

$$k = \frac{\sum_i^n (Bi \times Fi)}{(Rq \cdot \text{Days}) - En},$$

where k = number of elk the range can support for the winter period,

n = number of principal forages,

Bi = consumable biomass of principal forage species i,

Fi = nutrient content of principal forage species i,

Rq = individual elk requirements; metabolic requirements for daily maintenance

Days = number of days elk occupy the winter range, and

En = endogenous reserves of nutrient.

We calculated confidence intervals for carrying-capacity estimates based on variance of forage biomass estimates. We treated estimates of forage quality and animal requirements as constants. This is a reasonable assumption for forage quality because variability in these estimates was small (Hobbs et al. 1981). Because we viewed estimates of carrying capacities as a range evaluation procedure, we wished to eliminate variability due to individual animal differences in metabolic requirements.

Quantity and Quality of Forage

Principal forages (Petrides 1975) were defined as species contributing 2% or more of elk diets during any winter month. These species were identified by observing diet choices of tame, trained elk grazing on the winter range during each month from November through March 1976–77 and 1977–78 (Hobbs et al. 1981). Principal forages accounted for 92% of overwinter diets.

Biomass of principal forages was estimated at the end of the growing season (15–30 Aug) during 1976 and 1977. Thirty-two 1-ha stands of vegetation, stratified by habitat types and randomly located within strata, were each sampled with 30 0.25-m² plots for forbs, grasses, and fallen leaves of shrubs, and 10 2.0-m² plots for current stem growth of shrubs. Herbaceous material was clipped at ground level; shrub production was collected between ground level and 2.5 m high. All species were individually separated, dried at 100 C for 48 hours, and weighed to the nearest 0.1 g. Mean values for biomass of principal forages within a habitat type were multiplied by the area of that type and summed across types to estimate total winter-range biomass. Habitat areas were estimated by planimeter measurement of vegetation maps prepared

from aerial photos and ground surveys (D. Stevens, unpubl. data).

Nitrogen concentration and in vitro dry-matter digestibility (IVDMD) of principal forages were determined according to procedures described in Hobbs et al. (1981); gross energy of forages was determined by bomb calorimetry. Metabolizable energy (ME) of forage species was estimated by ME = gross energy × IVDMD × 0.85. This calculation provides a reasonable estimate of ME because IVDMD and percent in vivo energy digestibility can be assumed to be approximately equal (Moir 1961, Rittenhouse et al. 1971, Ruggerio and Whelan 1976, Milchunas et al. 1978), and because ME is consistently about 85% of digestible energy (Smith 1971, Thompson et al. 1973, Mautz et al. 1974, Simpson 1976). True digestible nitrogen was estimated as the product of nitrogen content and estimated true nitrogen digestibility, 0.90 (Robbins 1973:Table 26).

Range Supply of Energy and Nitrogen

Range supply of ME was calculated as the sum of products of forage biomass values multiplied by their ME content. Nitrogen supply was determined similarly, except that forages that contained less than 5.6 g N/kg of dry matter (3.5% crude protein) were excluded from the summation. Exclusion of these forages was based on the following reasoning. Elk lose 5.6 g N/kg of endogenous nitrogen in feces for each kilogram of dry matter they eat (Mould and Robbins 1981). Consequently, the nitrogen cost of digesting forages that contain less than 5.6 g N/kg exceeds their nitrogen contribution. Because consumption of these forages results in a net loss of nitrogen from the animal, we assumed they do not contribute to range nitrogen supply.

There are problems with this assumption. High-nitrogen foods could be mixed in elk diets with forages of lower nitrogen concentration and thereby exceed the nitrogen costs of digestion. We lack sufficient data to quantify how much of this "mixing" could occur. The extent to which metabolic fecal nitrogen is an obligate loss, independent of dry-matter intake, is uncertain, but it appears that endogenous nitrogen is excreted by the fasting animal (C. Schwartz and W. Regelin, pers. commun.). Moreover, our assumption treats all forages containing <5.6 g N/kg as equally poor sources of nitrogen. Although consumption of any of these forages would lead to negative nitrogen balance, lower nitrogen forages would exacerbate this imbalance more than those containing nitrogen concentrations close to 5.6 g N/kg. Despite these problems, we decided that eliminating low-nitrogen forages biased our estimate of range supply substantially less than assuming all forage, regardless of its nitrogen content, could permit nitrogen equilibrium in the animal.

Endogenous Energy and Nitrogen Reserves

Based on studies of several North American and European cervids (Anderson et al. 1972, Robbins et al. 1974, McEwan 1975, Simpson 1976), we inferred that elk entering the winter would likely have fat reserves averaging 15% of their body weight. Following the reasoning of Mautz et al. (1976), we assumed that catabolism of 1 g of fat provides energy equivalent to 6 kcal of ME intake.

Nitrogen reserves were much more difficult to estimate. However, it is known that when dietary protein is deficient, lean body is readily catabolized to meet nitrogen requirements (reviewed by Swick and Benevenga 1977). Although

nitrogen reserves in wild ruminants are not well characterized, we assumed (for use in sensitivity analysis) that elk could mobilize 10% of lean body, and that 1 g of lean tissue yields 4.8 kcal of metabolizable energy (Kleiber 1975:270).

Elk Energy and Nitrogen Requirements

We assumed that no costs for lactation or growth were incurred by elk during winter (Hobbs 1979, Robbins et al. 1981). Energy and nitrogen requirements for maintenance were based on a weighted mean elk body mass (200 kg) derived from data on the age and sex structure of the resident herd (D. Stevens, pers. commun.) and elk body-weight data of Dean et al. (1976). Carrying-capacity estimates are reported in units of 200-kg animals.

Daily energy requirements for maintenance were calculated from energetics data of Gates and Hudson (1978) coupled with elk activity budgets. Activity patterns of elk (time spent feeding, resting, and traveling) were determined by continuous monitoring of 2–5 elk fitted with radiotelemetry activity collars (Telonics Inc., Mesa, Ariz.) for 3 24-hour periods during each month from November through March 1979. Time spent in each activity was multiplied by the estimated energy cost of that activity, and the costs summed over 24 hours (Table 1). Simulation modeling indicated that during the 2 winters studied, thermoregulatory costs for elk were insignificant (Swift et al. 1981).

Nitrogen requirements for maintenance were equal to the amount of nitrogen of metabolic origin in the urine and feces. We based these requirements on losses of endogenous nitrogen, because forage nitrogen supply was calculated on the basis of true rather than apparent nitrogen digestibility. We assumed that

Table 1. Calculations of daily energy requirements for 200-kg elk.

Activity	Time spent in activity (hours/day)	Energy cost[a] (kcal/kg/hour)	Daily cost (kcal)
Feeding[b]	11.38	2.37	5,394
Bedding	9.77	1.03	2,013
Traveling[c]	2.85	3.12	1,778
Total			9,185

[a] Data from Gates and Hudson 1978.
[b] Assuming 2 km/hour walk.
[c] Assuming 4 km/hour walk.

maintenance nitrogen requirements would be met when true digestible nitrogen intake equaled endogenous nitrogen losses. Because true nitrogen digestibility does not account for losses of diet nitrogen in urine, this assumption may slightly underestimate nitrogen intake requirements necessary for nitrogen equilibrium. Metabolic fecal nitrogen excretion rate was approximated as 5.6 g N/kg dry-matter intake (Mould and Robbins 1981). We assumed that elk voluntary intake was limited by rumen fill on diets of the nutritional quality we observed (Hobbs et al. 1981). Intake levels were estimated as 5.0 kg/day for the calculation of metabolic fecal nitrogen excretion (Hungerford 1948, Geis 1950, Hobbs 1979:82). Endogenous urinary nitrogen was estimated as 0.16 g N/day/kg $wt^{0.75}$ (Mould and Robbins 1981). Thus, total maintenance nitrogen requirements for a 200-kg elk were approximated as 36.0 g N/day.

Gestation requirements for energy and nitrogen were estimated according to formulations of Robbins and Moen (1975), assuming 180 days of gestation on the winter range and a 12-kg fetus at term.

Sensitivity Analysis

A baseline prediction of total winter-range carrying capacity was calculated according to the model described above.

For this estimate, we used energy and nitrogen requirements for maintenance, and assumed no weight loss by wintering elk. The baseline estimate was then compared to recalculated carrying capacity based on adjusted model parameters to examine sensitivity of the model predictions to changes in animal requirements. These adjustments were

1. To examine the importance of endogenous reserves, the caloric value and nitrogen content of 90% of elk fat reserves and 10% of lean body was subtracted from overwinter requirements.
2. Energy and nitrogen costs of gestation were added to maintenance requirements of the adult female portion of the herd.
3. Metabolic fecal nitrogen rates were increased by 25%. Confidence intervals on the estimate of this rate (Mould and Robbins 1981) suggest such an increase is plausible.
4. To compare model sensitivity to changes in energy costs relative to nitrogen requirements, activity and bedded energy requirements were incremented by 25%.

RESULTS AND DISCUSSION

Principal forage species included 9 grasses, 5 shrubs, and 1 forb; these species contributed 2.45×10^9 kcal of ME and 11.0×10^3 kg nitrogen to total range supply during 1976–77, and 1.64×10^9 kcal ME and 6.6×10^3 kg nitrogen the following year (Table 2). Seventy-five percent of elk forage nitrogen and 86% of energy was contained in graminoids. We observed large annual differences in winter-range carrying capacity. Carrying capacity calculated from forage energy supply was $1,481 \pm 158$ (90% CI) during Year 1 and 991 ± 102 elk (67% as many) during Year 2. Carrying capacity based on nitrogen showed greater annual variation;

during Year 1 the winter range could support an estimated $1,674 \pm 165$ elk at maintenance, whereas the following year 39% as many, 994 ± 101 animals, could be carried. These temporal differences appeared to result from effects of decreased precipitation on Year 2 forage supplies (Hobbs 1979:84–85). Our estimates are reasonable given existing, stable population levels of 1,500–1,600 animals (G. Bear and R. Green, unpubl. rep., Colo. Div. Wildl. Fed. Aid Proj. W-126-R-3, 1980).

Our narrow confidence intervals indicate that our estimates are repeatable, but allow no inference of their accuracy because there are sources of bias in these predictions. At voluntary intake levels of 5.0 kg/day, elk diets would have to contain 1.8 kcal/g ME and 7.3 g/kg nitrogen to allow maintenance based on estimates of nutrient requirements. Shrubs contained concentrations of nitrogen adequate for maintenance, but were deficient in ME. Grasses offered adequate ME, but contained insufficient levels of nitrogen. Consequently, our baseline estimates of carrying capacity overestimate the number of animals that could be supported at maintenance. Realized nutritional status will depend on how forages are mixed in the diets (Hobbs 1979) and on the length of winter (Wallmo et al. 1977).

An additional bias results from probable declines in forage biomass during the winter incurred by trampling, shattering, and wind losses. Such decrements can be substantial (Pieper et al. 1974); because we did not account for these losses, our baseline estimates are inflated.

Moreover, the levels of precision we report may be much more difficult to obtain for estimates of carrying capacity for ungulates that feed more selectively than elk. Relatively common graminoids dom-

Table 2. Contribution of principal elk forages to winter-range metabolizable energy (ME) and nitrogen supply in Rocky Mountain National Park, Colorado, during 1976–78.

Forage[a]	Year[b]	Biomass[c] (kg × 10⁹)	Forage concentration		Range supply	
			ME[d] (kcal/g)	Nitrogen[e] (g/kg)	ME (kcal × 10⁶)	Nitrogen (kg)
Graminoids						
Bromus inermis	1977	10	1.6	6.0	16	60
	1978	f	f			
Bouteloua gracilis	1977	50	1.4	6.6	70	330
	1978	40	1.6	6.2	64	248
Calamagrostis canadensis	1977	320	1.5	6.8	480	2,176
	1978	210	1.5	5.7	315	1,197
Carex spp.	1977	500	1.6	6.2	800	3,100
	1978	400	1.5	6.6	600	2,640
Juncus balticus	1977	f	f			
	1978	30	1.4	4.4	42	g
Muhlenbergia montana	1977	240	1.5	5.7	360	1,368
	1978	100	1.6	5.6	160	560
Phleum pratense	1977	80	1.8	6.0	144	480
	1978	10	1.8	5.6	18	g
Poa pratensis	1977	40	1.7	7.2	69	288
	1978	30	1.6	5.8	48	174
Stipa comata	1977	60	1.7	7.1	102	426
	1978	60	1.7	5.7	102	342
Browse						
Populus tremuloides (leaves)	1977	60[h]	1.8	8.1	108	486
	1978	60	1.6	5.6	95	g
Potentilla fruticosa (stems)	1977	6	1.1	7.8	7	47
	1978	5	1.1	6.6	5	33
Purshia tridentata (stems)	1977	80	1.5	12.0	120	960
	1978	40	1.2	9.8	48	392
Rosa woodsii (stems)	1977	10	1.5	7.1	15	71
	1978	10	1.4	6.6	14	66
Salix spp. (leaves)	1977	20[h]	1.3	8.6	26	172
	1978	20	1.1	8.9	22	178
Salix spp. (stems)	1977	60	1.7	11.7	102	702
	1978	50	1.5	8.6	75	430
Forbs						
Erigononum umbellatum	1977	30	1.0	11.2	30	366
	1978	30	1.0	9.1	30	273
Total supply	1977				2,449	11,002
	1978				1,639	6,536

[a] Species contributing 2% or more to elk winter diets (Hobbs et al. 1981).
[b] 1977 = winter of 1976–77; 1978 = winter of 1977–78.
[c] Total biomass on winter range. For individual habitat data see Hobbs (1979).
[d] ME = gross energy × in vitro dry-matter digestibility (IVDMD) × 0.85. IVDMD data from Hobbs et al. (1981).
[e] Nitrogen = N content × 0.90. N content data from Hobbs et al. (1981).
[f] Not in diet.
[g] Includes only those species that contain greater than 5.6 g N/kg. Values not reported for forages containing less than this amount.
[h] Estimate based on 1977–78 data.

inated elk diets. The biomass of such forages can be estimated more precisely than the biomass of rare food items at the same level of sampling intensity.

Despite these problems, our estimates are useful for comparative purposes. There were large differences in the relative capability of upper montane habitat

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Table 3.   Carrying-capacity estimates for elk winter-range plant communities in Rocky Mountain National Park, Colorado, 1976-78.

| Habitat type | Year[a] | Carrying capacity (elk/day/ha)[b] | | | |
| | | Energy based | | Nitrogen based | |
		$\bar{x}$	90% CI	$\bar{x}$	90% CI
Grassland	1977	47	14	54	12
	1978	37	8	36	7
Mesic meadow	1977	241	85	246	89
	1978	90	18	91	12
Ponderosa pine-shrub	1977	47	8	61	10
	1978	27	5	34	8
Sagebrush	1977	47	13	54	12
	1978	27	4	27	6
Willow	1977	371	76	414	24
	1978	306	62	343	21
Aspen	1977	202	48	210	15
	1978	121	37	112	9
Wet shrub meadow	1977	299	76	314	24
	1978	117	19	130	15
Wet grass meadow	1977	227	39	233	10
	1978	170	14	173	12

[a] 1977 = winter of 1976-77; 1978 = winter of 1977-78.
[b] Units are 200-kg animals. This weight is based on a mean body mass weighted by age and sex structure of the resident herd.

types to support elk (Table 3). During both years, the more hygric communities (willow, wet shrub meadow, wet meadow) could carry the most elk, mesic communities (aspen and mesic meadow) were intermediate in their carrying capacity, and dry areas (grassland, ponderosa pine-shrub, and sagebrush) could support the fewest animals.

Estimates of carrying capacity in these habitat types were not closely related to the nutritional quality of winter diets selected there (Hobbs et al. 1981). Differences in energy-based carrying capacity accounted for only 25% of the variation in elk diet IVDMD. There was no significant relationship ($P = 0.48$) between nitrogen-based carrying capacity and dietary protein concentration. This lack of relation can be explained by the following reasoning. Carrying capacity estimated by the model used here is determined by the total amount of energy and nitro-

gen present. Diet quality, in contrast, is more closely related to the concentration of nutrients in individual food items and the relative selectivity of the animal. The poor correlation between diet quality and carrying capacity supports the hypothesis of White (1978) and the findings of Wallmo et al. (1977) that the relative quality of foods may be as important as their absolute abundance in determining habitat quality and supportable animal density. Carrying-capacity estimates that reflect both individual animal condition and population density must account for the amounts of foods of different nutrient concentrations as well as for the total amount of food that is available.

The results of the sensitivity analysis (Table 4) demonstrated which parameters were most important in determining our estimates. These are the parameters that must be estimated accurately if the model is to make useful predictions. Pa-

Table 4. Elk carrying-capacity estimates for winter range in Rocky Mountain National Park, Colorado, 1976–78.

Conditions	Year[b]	Estimated carrying capacity (200-kg elk)[a]		Percent change from baseline	
		Energy based	Nitrogen based	Energy based	Nitrogen based
Baseline[c]	1977	1,481	1,674		
	1978	991	994		
Add gestation costs[d]	1977	1,479	1,671	0	−1
	1978	990	984	0	−1
Lose 90% fat, 10% lean body	1977	1,657	1,900	+12	+13
	1978	1,109	1,128	+12	+13
Increase metabolic fecal N by 25%	1977	1,478	388	0	−77
	1978	989	141	0	−86
Increase activity energy costs by 25%	1977	1,330	1,674	−10	0
	1978	890	994	−5	0
Increase bedded energy costs by 25%	1977	1,404	1,674	−5	0
	1978	939	994	−5	0

[a] Units chosen based on weighted mean body mass weighted by age and sex structure of the resident herd. Estimate assumes a 180-day occupancy of the winter range. To convert to elk days per hectare, multiply by 0.09.
[b] 1977 = winter of 1976–77; 1978 = winter of 1977–78.
[c] Estimate based on measured energy and nitrogen supply and best approximations of elk requirements, assuming no weight loss. All other conditions are specified relative to baseline parameters.
[d] Assuming 65% of herd is female, and that the period of gestation on winter range = 180 days.

rameters to which the model is less sensitive need be estimated less well. This is useful in terms of determining future research direction. Sensitivity analysis showed predictions of the range supply–animal demand algorithm to be extremely responsive to changes in metabolic fecal nitrogen excretion rates; a 25% increase in this parameter reduced estimates of carrying capacity by 74–86%. In comparison, proportionally equal changes in energy costs of activity and resting had relatively small effect, reducing carrying-capacity estimates by 10 and 5%, respectively.

The pronounced influence of metabolic fecal nitrogen results from its simultaneous effect on animal requirements and range supply. Increasing this rate by 25% elevated nitrogen lost in the feces to 7 g N/kg dry-matter intake. If the animal excreted nitrogen at this rate, the only forages that could contribute nitrogen in excess of the amount lost were browses and a very few grasses. This effect is exacerbated because total nitrogen requirements were elevated from 36.5 to 50 g N/day. Consequently, the animal needs more nitrogen and has less food that can provide it.

Catabolism of endogenous reserves increased carrying capacity by 12% based on energy and 13% based on nitrogen. Thus, these reserves had a relatively small impact on total supportable animal density; maximum standing crops of animals in poor condition could be only slightly larger than those at maintenance. This does not mean that these reserves are not important to individual animal survival; they doubtlessly are, but it is important that these large differences in animal condition appear to have small effects on estimated carrying capacity.

CONCLUSIONS

Wiens (1977) observed that a potent force affecting animal populations is periodic deficits in resource supply. We demonstrate that such deficits do occur

for elk on winter range. Range resources and predicted supportable animal density were markedly variable between years. This variation has important implications for management and for implementation of the carrying-capacity model.

When resource supply fluctuates from year to year, managers should anticipate variation in animal numbers and individual animal condition unless populations are maintained well below maximum carrying capacity. Thus, carrying capacity should be viewed as a labile rather than a static characteristic of the habitat.

This variability must be remembered in designing future research for use in nutritional carrying-capacity estimates. That is, in the face of large annual changes in resource supply, it may not be necessary to measure other model inputs as precisely as is sometimes advocated. In a serial calculation like carrying capacity, the outcome is only as precise as the least precise input (Simpson et al. 1960:5–9); we contend annual variation in resource supply will usually limit the precision of long-term carrying-capacity estimates in the Rocky Mountain region.

This does not mean that accuracy of estimates of animal requirements and range supply should not be improved. But some of these parameters, as was demonstrated in the sensitivity analysis, are far more significant to model predictions than are others. For example, we recommend that studies of elk maintenance nitrogen requirements and energy–nitrogen interactions precede further study of energetics alone. This follows from the logic of Mautz (1978:322–323), who contended that we should study parameters about which we know least. In addition, we hold that study of sensitive parameters, those variables that are the most important determinants of nutrition-

al carrying capacity, should be given priority.

We conclude that nutritionally based estimates of carrying capacity offer a valuable procedure for evaluation of elk habitat. That is, they provide accountable estimates of the quality of ungulate ranges based on measurable attributes of the habitat that are directly related to individual animal condition and population performance. Specific features of that relation are still uncertain, but this uncertainty should not preclude use of carrying-capacity estimates for comparative purposes and range evaluation. We caution, however, that annual variability in resource supply and possible inaccuracy in model parameters may limit the predictive value of these procedures in the absence of long-term studies and improved input data.

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