ESTIMATES OF HABITAT CARRYING CAPACITY INCORPORATING EXPLICIT NUTRITIONAL CONSTRAINTS

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Abstract: We offer an algorithm for estimating supportable densities of herbivores consuming diets at different levels of nutritional quality. We use this procedure to predict carrying capacity of burned and unburned mountain shrub habitat for mule deer (*Odocoileus hemionus*) and mountain sheep (*Ovis canadensis*) and compare our predictions with those of traditional range supply/animal demand models. Unburned areas had higher carrying capacities for animals consuming low quality diets, but burned areas could support more animals on a high plane of nutrition. Traditional procedures for estimating carrying capacity failed to detect these interactions between carrying capacity and animal nutritional status. We conclude that reliable evaluation of relationships between range food supplies and animal food requirements must treat forage amount and quality as integrated rather than distinct features of habitat.

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Many decisions in range and wildlife management depend on reliable assessment of the quality of habitat. Estimates of habitat carrying capacity based on range food supply and animal food requirements have been used to evaluate habitats for wild herbivores (Mentis and Duke 1976, Wallmo et al. 1977, Hobbs et al. 1982, Potvin and Huot 1983). Although this approach is useful for comparing maximum supportable densities of animals among areas and time periods, it fails to relate the number of animals that can be supported to the nutritional status of individuals. This failure results from a simplifying assumption implicit in current procedures for estimating carrying capacity on a nutritional basis. Models of range supply and animal demand assume that food resources represent a single, homogeneous quantity (usually estimated as the sum of forage dry matter, energy, or nitrogen), which is partitioned among individuals according to their nutritional needs.

This assumption is clearly incorrect. The nutritional quality of herbage is inversely related to its abundance in many ecosystems (reviewed by White 1978, Mattson 1980, Breman and deWit 1983, Demment and VanSoest 1983). Because the abundance of food varies as a function of its quality, food-based predictions of habitat carrying capacity must consider the quality of diets obtainable by populations of animals using the habitat in question. Here, we offer a procedure for estimating carrying capacity of habitats for animals consuming diets at different levels of nutritional quality. We use the technique to evaluate burned and unburned mountain shrub communities for mountain sheep and mule deer, and illustrate its utility by comparing our estimates with predictions based on traditional range-supply/animal-demand procedures.

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METHODS

An Algorithm for Estimating Carrying Capacity

The concentration of nutrients in diets is frequently the primary variable influencing the condition of herbivores (White 1978). Dietary nutrient concentration is determined by the quality of available food items and by the mixture of those items in the diet. Dietary mixing is an important process. For example, if a deer requires a diet containing 7% crude protein to maintain protein balance, it can compensate for foods containing less than 7% by eating those with protein exceeding 7%. Although this process is an obvious part of diet selection, it causes ambiguities in estimating food supply. That is, although we might estimate the amount of forage containing 7% protein, such an estimate fails to predict the amount that can be *mixed* to obtain an overall diet concentration of 7%.

The question we address is this: How much food is present in the environment that will allow a population of animals to obtain diets averaging a specific level of some nutrient? To answer this question we must know how the nutrient is distributed within the available forage. A hypothetical example of such a nutrient distribution (Fig. 1) will clarify the question and its solution. Forage biomass (y) is defined as some $f(x)$ where x is a nutrient concentration. The specified level of the nutrient that animals must obtain is CONC. X_{max} is the highest nutrient concentration in an available food item. We are interested in finding the point X_1 such that the average nutrient content of forages to the right of X_1 is CONC. This point defines the *maximum* amount of forage that can be combined to yield the specified nutrient concentration. By specifying CONC, we can solve for X_1 in the following equation:

$$\text{CONC} = \frac{\int_{X_1}^{X_{max}} x f(x)\, dx}{\int_{X_1}^{X_{max}} f(x)\, dx}.$$

Having found X_1, we can find MAX, the maximum amount of forage that can be combined to yield the nutrient concentration CONC:

$$\text{MAX} = \int_{X_1}^{X_{max}} f(x)\, dx.$$

Although this is the exact solution to the problem, it is unlikely that we will be able to define a nutrient distribution [$f(x)$] for a field situation with precision sufficient to implement it. There is however, an analogous discrete solution that can be applied to data collected in the field. We obtain data on the biomass and nutrient concentration of foods eaten by the animal species we are interested in (B_i = biomass of the ith food category, N_i = nutrient concentration of the ith food category). Given these paired data, we arrange them in descending order of nutrient concentration, and sum the biomass until adding another category causes the nutrient concentration of the summed biomass to be less than or equal to CONC. The number of food categories included when this constraint is met = t:

$$\frac{\sum_{i=1}^{t} (N_i B_i)}{\sum_{i=1}^{t} B_i} \le \text{CONC}.$$

If the concentration of the summed biomass

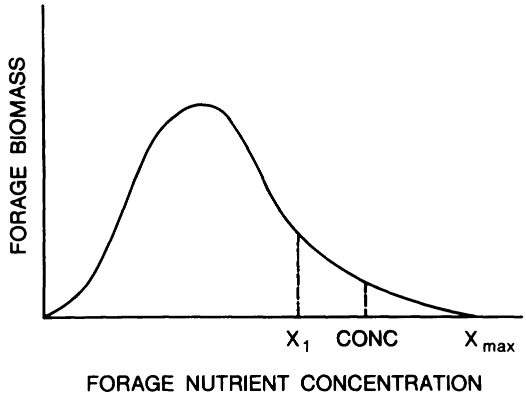

Fig. 1. Hypothetical nutrient distribution relating forage amount to forage biomass. CONC is defined as a specific level of forage nutrient concentration. X_{max} is the maximum concentration of nutrient found in any forage item. X_1 is a point such that the mean nutrient concentration of the biomass to the right of X_1 = CONC.

equals CONC, then MAX = $\sum_{i=1}^{t} B_i$. However, it will usually be the case that addition of the last biomass category (B_t) will cause the concentration of the summed biomass to be less than CONC, i.e.:

$$\frac{\sum_{i=1}^{t-1} (N_i B_i) + N_t B_t}{\sum_{i=1}^{t-1} B_i + B_t} < \text{CONC}.$$

We then need to estimate how much biomass from category t can be added to make this relationship an equality. Call that amount ADD_t; we can solve for it directly:

$$\frac{\sum_{i=1}^{t-1} (N_i B_i) + \text{ADD}_t(N_t)}{\sum_{i=1}^{t-1} (B_i) + \text{ADD}_t} = \text{CONC}$$

$$\sum_{i=1}^{t-1} N_i B_i + \text{ADD}_t(N_t) = \text{CONC}\left(\sum_{i=1}^{t-1} B_i\right) + \text{CONC}(\text{ADD}_t)$$

$$\text{ADD}_t(N_t) - \text{CONC}(\text{ADD}_t) = \text{CONC}\left(\sum_{i=1}^{t-1} B_i\right) - \sum_{i=1}^{t-1} N_i B_i$$

$$\mathrm{ADD}_t(N_t - \mathrm{CONC}) = \mathrm{CONC}\left(\sum_{i=1}^{t-1} B_i\right) - \sum_{i=1}^{t-1} N_i B_i$$

$$\mathrm{ADD}_t = \frac{\mathrm{CONC}\left(\sum_{i=1}^{t-1} B_i\right) - \sum_{i=1}^{t-1} N_i B_i}{(N_t - \mathrm{CONC})}.$$

Once we know ADD_t, then:

$$\mathrm{MAX} = \sum_{i=1}^{t-1} B_i + \mathrm{ADD}_t,$$

and carrying capacity can be estimated for animals consuming diets averaging CONC by dividing MAX by individual dry matter intake rates (INTAKE): Carrying Capacity (animal days/ha) = MAX (kg/ha) ÷ INTAKE (kg/animal/day). An example of these calculations is given in Table 1.

This approach to carrying capacity is based on two important assumptions. First, it assumes that herbivores will select higher quality forage items in preference to lower quality ones. Specifically, for any solution for diet nutrient levels = CONC, we must assume that animals do not choose foods with nutrient levels less than N_t. Most optimal foraging models invoke similar assumptions (reviewed by Pyke et al. 1977). Although ample empirical evidence supports the notion that herbivores prefer high quality foods (reviewed by Klein 1970, White 1978, Owen-Smith 1982), they probably are not as constrained in their choices as this assumption requires. Moreover, plant defense compounds may influence diet selection to a greater extent than forage nutritional value (Bryant and Kuropat 1980). The importance of this assumption to interpreting predictions of the model depends on how those predictions are used. Our model reliably predicts the maximum number of animals that can obtain diets of a specified quality level *or* the maximum quality of diets obtainable by a specified number of animals. We do not attempt to predict realized diet quality as a function of animal numbers because other variables may also influence diet selection. However, as we will point out later, predictions of our model are plausibly related to observed diet selection patterns of wild ungulates.

The second necessary assumption is that our list of forage categories must reflect distinctions animals make among forage items, for example among plant parts as well as plant species. If animals distinguish among forage items (e.g., grass leaves vs. culms) and those items are lumped together in a single category (e.g., "grass"), variation in nutrient concentration among items is reduced. That variation is critical to the outcome of the algorithm. The exception to this assumption occurs when there is little or no variation in N_i among a particular set of forage items. When that is the case, those items can be pooled and their biomass and nutrient concentration can be estimated collectively. To continue the example, leaves of different species of palatable grasses at the same phenological stage can be considered a homogeneous category because there is relatively little interspecific variation in nutrient content among grass leaves. However, leaves and culms of the same plant differ in nutritional quality and must be separated into distinct categories if the animal chooses between them.

Application of the Algorithm

We used this procedure to estimate carrying capacity of burned and unburned mountain shrub communities for populations of mountain sheep and mule deer consuming diets differing in levels of nitrogen (N) and metabolizable energy (ME). We worked in a south-facing montane valley at 2,300 m elevation 1.5 km NE of Rustic, Colorado. We chose three pairs of 1-ha plots; members of each pair were similar in slope, aspect, soil moisture, and vegetative composition. We randomly assigned burn treatments to one member of each pair. Detailed description of the study area, fire prescriptions, and fire behavior were reported elsewhere (Hobbs and Spowart 1984).

We estimated aboveground biomass of principal foods (Petrides 1975) of mule deer and mountain sheep at the end of the growing season (20–30 Aug) 1 year following treatment. Principal foods were identified during grazing trials with tame mule deer and mountain sheep (Hobbs and Spowart 1984).

Biomass of forages was estimated by clipping 30 ¼-m^2 plots in each burn and control replicate, separating the plots' contents into principal food categories, drying them at 100 C for 48 hours, and weighing them to the nearest 0.1 g. Ten separate samples of each forage were

Table 1. Example calculations of a carrying capacity algorithm incorporating diet quality constraints.

Data: t	Forage	Biomass (kg DM/ha)	Nitrogen content (g N/g DM)
1	Grass leaves, green	150	0.025
2	*Eriogonum umbellatum*	50	0.020
3	Grass leaves, dead	400	0.015
4	*Purshia tridentata*, stems	80	0.014

Calculations:

(1) t = Number of forages that can be mixed such that the total mixture no longer exceeds 2.0% N.

$t = 1$,

$$\frac{\sum_{i=1}^{1} B_i N_i}{\sum_{i=1}^{1} B_i} = \frac{150 \times 0.025}{150} = 0.025$$

$t = 2$,

$$\frac{\sum_{i=1}^{2} B_i N_i}{\sum_{i=1}^{2} B_i} = \frac{(150 \times 0.025) + (50 \times 0.020)}{150 + 50} = 0.023$$

$t = 3$,

$$\frac{\sum_{i=1}^{3} B_i N_i}{\sum_{i=1}^{3} B_i} = \frac{(150 \times 0.025) + (50 \times 0.020) + (400 \times 0.015)}{150 + 50 + 400} = 0.018.$$

(2) Amount of category $t = 3$ that can be added to categories 1 and 2 such that the total amount has an N concentration equal to 2.0% N:

$$\text{ADD} = \frac{\text{CONC}\left(\sum_{i=t}^{t-1} B_i\right) - \sum_{i=t}^{t-1} N_i B_i}{(N_t - \text{CONC})}$$

$$= \frac{(0.02) \times (150 + 50) - (150 \times 0.025) + 50(0.020)}{0.015 - 0.020}$$

$$= 150 \text{ kg}.$$

(3) Total amount of forage that can be mixed such that the concentration of the mixture = 2.0% N:

$$\left(\sum_{i=1}^{t-1} B_i\right) + \text{ADD} = (150 + 50) + 150 = 350 \text{ kg}.$$

(4) Assuming dry matter intake rate of 1.5 kg/day, carrying capacity for animals consuming diets with N concentrations of 2.0%:

$$350 \div 1.5 = 233 \text{ animal days/ha}.$$

also collected from each replicate, composited, and stored at −10 C. These samples were dried at 50 C for 48 hours and analyzed for dry matter, ash, and N content according to the Association of Official Analytical Chemists (1970). In vitro digestible dry matter (IVDDM) of these samples was determined following the procedure of Tilley and Terry (1963) as modified by

Table 2. Nutritional requirements of mule deer and mountain sheep used to estimate carrying capacity.

Species	Requirements	Reference
Mule deer[a]	Dry matter intake = 1.5 kg/day	Alldredge et al. 1974
	Nitrog	bins et al. 1974
	Energ	tz et al. 1983
Mountain sheep[a]	Dry m	ert 1973
	Nitrog	ert 1973
	Energ	ppel and Hudson 1979

[a] Assuming average mule deer weight = 60 kg and
[b] Nitrogen requirement estimated as endogenous u
[c] Energy requirement estimated as 2× standing m

To create distribution for fitting:
1) get nutrient concentration by dividing ME by DM.
2) create kg/ha number of jittered samples

Pearson (1970) using innoculum fr lated Holstein cow fed alfalfa (*Me va*) hay. Forage ME was estimated as gross energy × 0.85. The rationale

by Wallmo et al. (1977) 2). d available that allowed levels was calculated ac-

Table 3. Range supply of dry matter (DM), metabolizable energy (ME), and nitrogen (N) in mountain sheep and mule deer foods from burned and unburned mountain shrub communities.

Plant species	Plant part[a]	Animal species[b]	DM (kg/ha) Burn	DM (kg/ha) Control	ME (Mcal/ha) Burn	ME (Mcal/ha) Control	N (kg/ha) Burn	N (kg/ha) Control
Grasses	gl	D, S	66.9	122.5	166.4	197.2	1.59	2.44
	dl	S	18.3	50.4	37.4	71.6	0.40	0.96
	cl	S	18.1	32.9	17.1	22.7	0.31	0.48
	in	S	11.0	12.9	16.1	15.2	0.18	0.20
Forbs								
Agoseris glauca	w	D, S	7.9	0.5	12.3	0.4	0.17	0.01
Antennaria parvifolia	w	D, S	4.3	5.5	8.7	7.9	0.09	0.10
Aster spp.	w	D, S	21.0	13.2	58.1	30.9	0.49	0.26
Chrysopsis spp.	w	D, S	75.5	45.5	136.7	63.3	1.58	0.87
Eriogonum umbellatum	in	D, S	10.7	0.6	14.9	0.5	0.12	0.01
	lf	D, S	13.4	15.2	25.8	22.6	0.16	0.11
Galium boreale	w	D, S	5.3	14.7	10.7	21.0	0.02	0.31
Geranium spp.	w	D, S	2.2	6.2	3.7	8.2	0.04	0.09
Lupinus greenei	lf	D, S	21.6	0.6	62.9	2.2	0.64	0.02
	st	S	21.0	2.4	18.7	0.9	0.35	0.04
	in	D, S	4.9	0.3	17.5	1.0	0.14	0.01
Potentilla spp.	w	D, S	22.8	15.2	36.7	19.2	0.53	0.21
Solidago nannum	w	D, S	3.3	0.5	7.3	0.8	0.07	0.01
Thermopsis divaricarpa	w	D, S	27.4	19.9	68.2	31.8	0.58	0.36
Shrubs								
Artemisia frigida	w	D	3.7	30.8	11.7	60.2	0.80	0.52
A. tridentata	lf	D	2.4	115.3	5.3	270.1	0.20	1.68
	st	D	3.0	26.2	2.0	2.3	0.20	0.40
	in	D, S	0.0	40.7	0.0	68.8	0.00	0.66
Purshia tridentata	lf	D	0.3	27.5	0.7	57.7	0.10	0.59
	st	D	0.0	11.9	0.0	13.5	0.00	0.09
	in	D	0.0	0.9	0.0	1.1	0.00	0.01
Ribes cereum	lf	D, S	2.4	18.5	5.1	15.5	0.03	0.18
	st	D, S	9.5	4.0	7.9	3.1	0.07	0.04
	in	D	0.0	0.6	0.0	0.5	0.00	0.01
Total, mule deer forage[c]			309.3 A	539.2 B	651.1 A	903.9 B	6.71 A	9.22 B
Total, mountain sheep forage[c]			367.4 A	426.0 B	761.9 A	740.1 A	7.30 A	6.10 A

[a] gl = green leaves; dl = dead leaves; cl = culm; in = inflorescence; w = whole plant; lf = leaves; st = stem, current growth.
[b] D = mule deer foods; S = mountain sheep foods.
[c] Means with different capital letters are significantly different at $P < 0.05$.

Table 4. Estimates of carrying capacity (animal/day/ha)[a] of burned and unburned mountain shrub communities for mule deer and mountain sheep. Estimates based on range supply ÷ animal requirements.

Species	Measure of range supply	$\bar{x}$ carrying capacity[b] Burn	Control
Mule deer	Dry matter	206 A	359 B
	Energy	141 A	195 B
	Nitrogen	578 A	794 B
Mountain sheep	Dry matter	193 A	221 A
	Energy	144 A	140 A
	Nitrogen	429 A	358 A

[a] Units are 60-kg mule deer and 75-kg mountain sheep.
[b] Based on average of three replicate plots. Means with different capital letters are significantly different at $P = 0.05$.

Table 5. Estimates of carrying capacity (animal/days/ha) of burned and unburned mountain shrub habitat based on the average concentration of nitrogen and metabolizable energy in diets of the animal populations supported.

Diet quality level	$\bar{x}$[a] carrying capacity: Mountain sheep		Mule deer	
	Burn	Control	Burn	Control
N (g N/100 g DM)				
3.00	15 A	1 B	24 A	1 B
2.75	40 A	1 B	58 A	2 B
2.50	96 A	3 B	126 A	4 B
2.25	147 A	9 B	191 A	124 B
2.00	192 A	17 B	206 A	210 A
1.75	193 A	54 B	206 A	344 B
1.50	193 A	204 A	206 A	359 B
1.25	193 A	221 A	206 A	359 B
ME (kcal/g DM)				
3.00	11 A	0 B	14 A	0 B
2.75	22 A	5 B	28 A	0 B
2.50	66 A	10 B	84 A	1 B
2.25	160 A	26 B	185 A	4 B
2.00	193 A	95 B	206 A	160 A
1.75	193 A	221 A	206 A	330 B
1.50	193 A	221 A	206 A	359 B

[a] Means with different capital letters are different at $P < 0.05$.

cording to the algorithm described above. Carrying capacity was estimated at each level by dividing food supply by the dry matter intake rate of a 75-kg mountain sheep, estimated as 1.9 kg/day (Hebert 1973; N. T. Hobbs, unpubl. data) or a 60-kg mule deer, 1.5 kg/day (Alldredge et al. 1974). Effects of treatment on estimates of carrying capacity were examined with paired *t*-tests.

Comparisons with Other Procedures

We also estimated carrying capacity of burned and unburned plots based on traditional range-supply/animal-demand models following procedures used by Hobbs et al. (1982). Total range supply was based on the standing crop of forage dry matter, ME, and N. Estimates of animal requirements are summarized in Table 2.

RESULTS

Fire reduced range supplies of dry matter, ME, and N in forages consumed by mule deer ($P < 0.05$, Table 3). This reduction resulted primarily from the large decrease in the standing crop of shrubs following burning. Range food supply for mountain sheep was less strongly influenced; although dry matter of sheep forages declined following burning ($P < 0.05$), the supplies of ME and N for sheep remained unchanged. Estimates of carrying capacity based on range-supply and animal demand reflected these differences (Table 4); unburned areas could support more deer than burns could, but burning had no effect on carrying capacity for mountain sheep.

Estimates of carrying capacity incorporating diet quality constraints revealed fundamental differences in the quality of burned and unburned habitats (Table 5). Controls could support few animals at high diet quality levels because they offered little forage that contained high levels of N and ME. In contrast, burns could support substantial numbers of mule deer and mountain sheep consuming high quality diets. Burns and controls were similar in their carrying capacities only at intermediate or low dietary nutrient concentrations.

Why are our estimates so different from those obtained by the traditional range-supply/animal-demand procedure? The divergence in predictions resulted from the way N and ME were distributed within forage standing crops; burns tended to have more forage with high nutrient concentrations but less forage overall (Figs. 2, 3). The procedure we offer responded to differences in these distributions of N and ME. Traditional procedures were sensitive only to differences in the total amount of forage and its mean nutrient concentration.

One feature of our estimates requires expla-

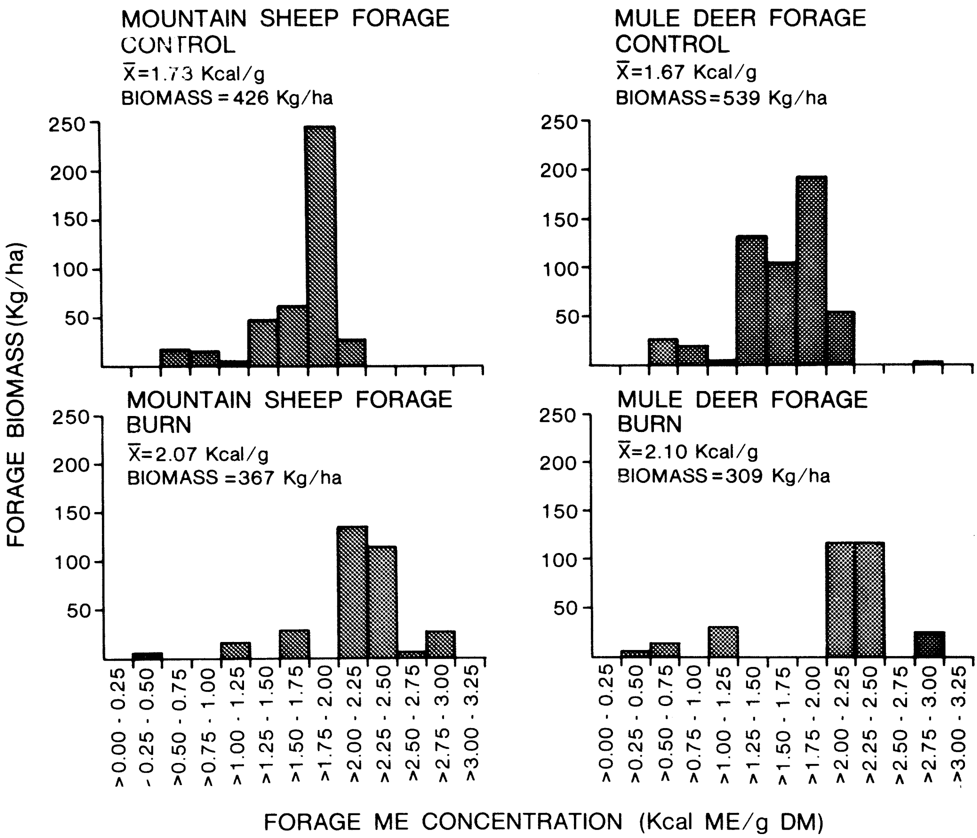

Fig. 2. Distribution of metabolizable energy (ME) in forages of mule deer and mountain sheep in burned and unburned mountain shrub habitat.

nation. Our estimates of carrying capacity increased as target diet quality declined until carrying capacity reached a maximum (Table 5) equal to the traditional estimate based on dry matter supply (Table 4). This convergence between the two methods resulted because maximum carrying capacity estimated by our algorithm occurred when diet N or ME concentration equaled the mean concentration in the standing crop of forage. When target diet quality levels fell to the overall level of the forage on offer, *all* the forage standing crop could be mixed in diets to allow that diet quality level. At that point, carrying capacity estimated by our procedure and by the traditional approach were based on *total* forage supply and individual dry matter intake.

DISCUSSION

We contend that forage quality × quantity interactions are fundamentally important in habitat management for herbivores. With few exceptions (Breman and deWit 1983, Demment and VanSoest 1983), forage quality and quantity have been measured as distinct variables. Such distinction prevents consideration of management objectives in habitat evaluation. For example, our results (Table 5) show that unburned habitat is superior to burned areas for supporting high densities of mule deer on a relatively low plane of nutrition. Burning becomes an efficacious treatment when management objectives specify carrying fewer animals at higher diet quality levels. The role of fire in meeting these objectives becomes obvious only when diet quality and food quantity are integrated in estimates of carrying capacity. Such integration can facilitate decisions on stocking densities of wild herbivores. Often, wildlife managers need to simultaneously achieve goals for individual animal condition as well as population density. Because these objectives are interdependent, it

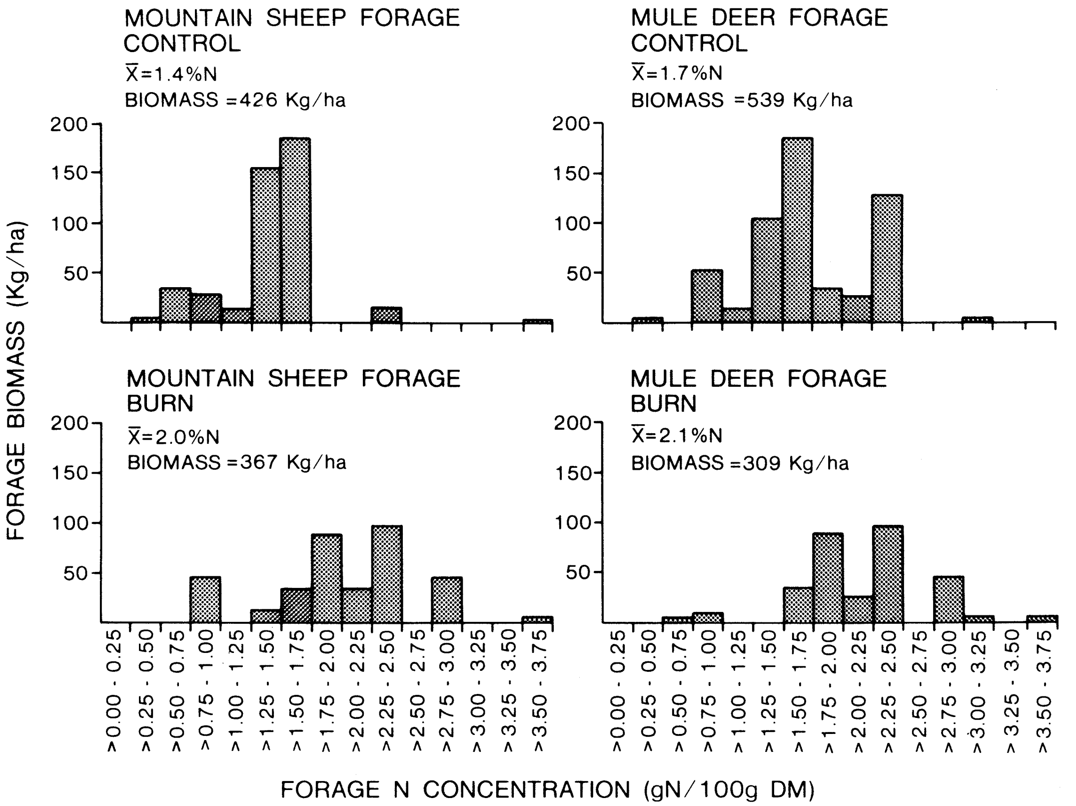

Fig. 3. Distribution of nitrogen (N) in forages of mule deer and mountain sheep in burned and unburned mountain shrub habitat.

is necessary to estimate population densities allowing appropriate levels of nutrition for individuals. Using this algorithm, a stocking rate appropriate to a specific nutritional plane can be approximated.

Our findings explain two seeming paradoxes in the literature on range carrying capacity. Wallmo et al. (1977) observed that the calculated carrying capacity of a particular deer winter range in Colorado was zero, an enigmatic observation because many deer survived there throughout the winter. In that case, carrying capacity was estimated at a diet quality level capable of supplying maintenance energy requirements. This diet quality level could not be provided by any of the forages in their analysis; thus, their calculated carrying capacity was zero. This situation is analogous to our present low estimates of carrying capacity on control plots when high quality diets are specified (Table 5). If Wallmo et al. (1977) had progressively relaxed their diet quality constraints and recalculated carrying capacity, they would have found a positive, non-zero value. This positive value for carrying capacity would have corresponded to diets of submaintenance quality, of course; but this is a realistic expectation for Colorado winter ranges.

A second paradox was reported by Hobbs et al. (1982), who found that carrying capacities of elk (*Cervus elaphus*) habitats were poorly related to the nutritional quality of elk diets selected in those habitats. The traditional range-supply/animal-demand model used to estimate carrying capacity could not respond to the way nutrients are distributed in available forages, but the diet selection process and its dietary outcome are greatly influenced by the shape of that distribution. In contrast, our present predictions of fire effects on carrying capacity of mountain shrub habitats—predictions dependent upon the distribution of nutrients—closely parallel reported effects of fire on nutrition of mule deer and mountain sheep grazing on the sample plots we studied (Hobbs and Spowart 1984).

We show that there exists an upper limit on the nutritional quality of diets obtainable by any given population, a limit that progressively declines as population density increases. This inverse relationship between the quality of diets obtainable and animal density demonstrates clearly the density-dependent nature of animal/forage interactions. Even when the total amount of forage available is not limiting, increases in animal density may compel deterioration in the nutritional status of individuals. Because these concepts are fundamental to management of wild ungulates and the habitats they occupy, they should be explicity represented in food-based procedures for habitat evaluation. Our algorithm incorporates principles of density dependence in estimates of range carrying capacity.

A productive endeavor in wildlife research has focused on the resolute description of nutritional requirements of animals, particularly wild ruminants (reviewed by Robbins 1983). An ostensible purpose of this undertaking has been to facilitate reliable prediction of the capability of habitats to support wildlife. Although this work is laudable, its use is becoming limited as our ability to estimate animal nutritional requirements outpaces our capability to describe the nutritional resources available to meet those requirements. The model we offer improves our ability to relate range forage resources to specific animal requirements.

LITERATURE CITED

ALLDREDGE, A. W., J. F. LIPSCOMB, AND F. W. WHICKER. 1974. Forage intake rates of mule deer estimated with fallout Cesium-137. J. Wildl. Manage. 38:508–516.

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1970. Official methods of analysis. 11th ed. Assoc. Off. Anal. Chem., Washington, D.C. 1015pp.

BREMAN, H., AND C. T. DEWIT. 1983. Rangeland productivity and exploitation in the Sahel. Science 221:1341–1347.

BRYANT, J. P., AND P. J. KUROPAT. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Annu. Rev. Ecol. Syst. II:261–285.

CHAPPEL, R. W., AND R. J. HUDSON. 1979. Energy cost of standing in Rocky Mountain bighorn sheep. J. Wildl. Manage. 43:261–263.

DEMMENT, M. W., AND P. J. VANSOEST. 1983. Body size, digestive capacity, and feeding strategy of herbivores. Windrock Int. Livestock Res. Publ. 66pp.

HEBERT, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. Thesis, Univ. British Columbia, Vancouver. 355pp.

HOBBS, N. T., D. L. BAKER, J. E. ELLIS, D. M. SWIFT, AND R. A. GREEN. 1982. Energy- and nitrogen-based estimates of elk winter-range carrying capacity. J. Wildl. Manage. 46:12–21.

———, AND R. A. SPOWART. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wildl. Manage. 48:551–560.

KLEIN, D. R. 1970. Food selection by North American deer and their responses to over-utilization of preferred plant species. Pages 25–44 *in* A. Watson, ed. Animal populations in relation to their food resources. Blackwell Sci. Publ., Oxford, U.K.

MATTSON, W. J., JR. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. 11:119–161.

MAUTZ, W. W., P. J. PEKINS, AND J. A. WARREN. 1983. Cold temperature effects on metabolic rate of white-tailed, mule, and black-tailed deer in winter. N.H. Agric. Exp. Stn. Sci. Contrib. 1214. 8pp.

MENTIS, M. T., AND R. R. DUKE. 1976. Carrying capacity of natural veld in Natal for large herbivores. S. Afr. J. Wildl. Res. 6:65–74.

OWEN-SMITH, N. 1982. Factors influencing the consumption of plant products by large herbivores. Pages 359–404 *in* B. J. Huntley and B. H. Walker, eds. Ecological studies. Vol. 42. Ecology of tropical savannas. Springer-Verlag, New York, N.Y.

PEARSON, H. A. 1970. Digestibility trials: in vitro techniques. Pages 85–92 *in* Range and wildlife habitat evaluation, a research symposium. U.S. Dep. Agric. For. Serv. Misc. Publ. 1147.

PETRIDES, G. A. 1975. Principal foods versus preferred foods and their relation to stocking rate and range condition. Biol. Conserv. 7:161–169.

POTVIN, F., AND J. HUOT. 1983. Estimating carrying capacity of a white-tailed deer wintering area in Quebec. J. Wildl. Manage. 47:463–475.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137–154.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, N.Y. 343pp.

———, R. L. PRIOR, A. N. MOEN, AND W. J. VISEK. 1974. Nitrogen metabolism of white-tailed deer. J. Anim. Sci. 38:186–191.

TILLEY, J. M. A., AND R. A. TERRY. 1963. A two stage technique for the in vitro digestion of forage crops. J. Br. Grassl. Soc. 18:104–111.

WALLMO, O. C., L. H. CARPENTER, W. L. REGELIN, R. B. GILL, AND D. L. BAKER. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122–127.

WHITE, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia 33:71–86.

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