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THESIS

COMPARATIVE WINTER NUTRITION OF ELK IN THE
JEMEZ MOUNTAINS, NEW MEXICO

Submitted by

Mary M. Rowland

Department of Fishery and Wildlife Biology

In partial fulfillment of the requirements

for the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 1981

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY MARY M. ROWLAND ENTITLED COMPARATIVE WINTER NUTRITION OF ELK IN THE JEMEZ MOUNTAINS, NEW MEXICO, BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

COMPARATIVE WINTER NUTRITION OF ELK IN THE JEMEZ MOUNTAINS, NEW MEXICO

Diet quality and nutritional status of elk (*Cervus elaphus nelsoni*) were studied in the Jemez Mountains, New Mexico, during January-April 1980. A recently burned montane area, including portions of Bandelier National Monument, and an unburned upper montane area in the Valle San Antonio were selected for winter range comparisons. Botanical composition of elk diets, determined by microhistological analysis of feces, was markedly different between the 2 areas. Grasses dominated diets in the burned area (\bar{x} = 90%), but were consumed in nearly equal proportions with browse in the unburned area (\bar{x} = 52%, grasses; \bar{x} = 41%, browse). Forbs were minor dietary components in both areas. Diet botanical composition did not vary during the winter and early spring.

Grasses were more digestible than was browse, but crude protein content was similar between forage classes. Temporal increases in quality of grasses were significant, whereas browse forages remained relatively constant in quality. Comparisons of forage protein and IVDOM (*in vitro* digestible organic matter) revealed no differences between locations.

Dietary protein ranged from 3.5-7.2% in Bandelier and from 4.7-7.5% in the Valle San Antonio, and was consistently superior in the unburned area. Increases in diet IVDOM in Bandelier (35% to 48%) surpassed those in the Valle San Antonio (33% to 39%) and were more rapid in Bandelier. Increases in diet quality were highly correlated with changes in quality of grasses consumed by elk. Observed disparities in diet quality between areas were caused primarily by differences in diet compositions and the

differing qualities of grasses vs. browse. Forage quality was more variable than was diet quality, indicating the ability of elk to maintain relatively constant diet quality when confronted with large fluctuations in forage quality.

A simulation model of ruminant energy and nitrogen balance was used to predict potential effects of diet quality on elk nutritional status. Greater energy deficits were predicted for elk in the unburned area, effecting greater losses of fat and lean body. Superior dietary nitrogen in the unburned area was insufficient to compensate for these losses.

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Division of Wildlife facilities for preparing forage samples for analysis. Don Reichert permitted use of the Rocky Mountain Forest and Range Experiment Station laboratory for forage analyses. He also assisted with the analyses, as did Daniel Milchunas, Beth Painter, and Donna Winn.

Don Hill prepared the figures, and Mary Jane Klepac keypunched data. The manuscript was typed by Kathy Everett.

I am especially thankful to my parents for their constant support of my education and aspirations.

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INTRODUCTION

Fire, logging, and other disturbances that reverse successional trends are important in maintaining habitats used by elk (Martinka 1976, Boyd 1978, Gruell 1979, Hunter et al. 1979). Preference for post-burn habitats has been observed for elk (Asherin 1976, Martinka 1976, Davis 1977, Lowe et al. 1978, Roppe and Hein 1978, Singer 1979) and may result from changes in forage quality and quantity, as well as alteration of cover characteristics. Increases in nutrient content (Dewitt and Derby 1955, Lay 1957, Vlamis and Gowans 1957, Duvall 1970, Hallisey and Wood 1976) and productivity (Vogl 1965, Leege 1969, Dills 1970, Nelson 1974) of forage in response to burning are common, although effects may vary with season, year, and forage species. Fire also induces conversion of forested habitats to earlier seral stages (Ahlgren and Ahlgren 1960, Weaver 1967, Leege 1968), thereby increasing abundance of herbaceous plants (Biswell 1972, Foxx and Potter 1978). Martinka (1976) believed that maximum benefit to elk was derived from shrub/forest mosaics that developed following fire, rather than from changes in plant nutritional quality.

The La Mesa fire of 1977 burned 6000 ha of potential winter range for Rocky Mountain elk in the eastern Jemez Mountains of New Mexico, near Los Alamos. A mixture of native grasses, seeded 1 month following the fire, produced dense swards on the burn (Potter and Foxx 1979). Establishment of seeded grasses was particularly successful in severely burned sites, which constituted over 90% of the total area burned (T. Foxx, pers. commun.). Sixteen months after the La Mesa fire, biomass of herbaceous plants in these sites was nearly 3 times that in lightly

burned areas, where native grasses dominated (Potter and Foxx 1979). A pre-fire study also revealed significantly greater biomass of herbs in burned vs. control plots in Bandelier National Monument, site of the La Mesa burn (Foxx and Potter 1978).

Elk use of the La Mesa burn has increased (White 1981). Prior to the fire, most elk in the Los Alamos area wintered on an area burned in 1954, approximately 5 km from the La Mesa site. Increased use of the La Mesa burn during winter 1978-1979 was a function of re-establishment of herbaceous forage, combined with an unusually severe winter (Conley et al. 1979). Elk continued to use the burn extensively during the winters of 1979-1980 and 1980-1981, despite exceptionally mild weather. Use of the 1954 burn has subsequently declined (White 1981). The increase in elk numbers on the La Mesa burn was initially a function of immigration, but increased productivity of elk wintering there may also have occurred.

Peaks in ungulate populations of the Rocky Mountains occurred 20-30 years after major fires (Leege 1968, Lyon 1969, Martinka 1976, Leege and Hickey 1977). As vegetation changed, however, subsequent population declines resulted, presumably from overuse of available habitat (Lyon 1969, Martinka 1976, Leege and Hickey 1977). Spencer and Hakala (1964) reported peaks in post-burn moose (*Alces alces*) populations, caused by increased production of calves and immigration of moose from surrounding winter ranges. Improved fecundity, presumably a result of improved nutrition of females, has also been reported for deer (*Odocoileus* spp.) (Nelson 1974) and red deer (*Cervus elaphus*) (Lowe 1971) following fire.

Concern for possible population responses of elk, resulting in alteration of local vegetation and increased man-elk interactions on

Los Alamos National Laboratory lands, prompted study of the La Mesa fire's impact on elk condition and diet quality. The only sizable elk herd in the immediate area wintered on the La Mesa burn. A second herd was located wintering in an unburned site at a higher elevation in the Jemez Mountains. Plant associations not occurring on the La Mesa burn were present in this area. The higher elevation winter range was selected for comparison with the perturbed La Mesa area. The 2 herds shared a common summer range (Weber 1981) and thus provided a unique opportunity to study effects of winter range condition on elk diets and nutritional status.

The Jemez Mountain elk summer in upper montane areas, but winter in herds throughout the Jemez Mountains and Pajarito Plateau, from sub-alpine to pinyon-juniper habitats (Fig. 1). Burned areas are characteristic of ponderosa pine (scientific names of plants are in Appendix A) habitats, which support much of the winter elk population. Comparing indexes of nutritional status of elk wintering in an unburned, upper montane area with similar measures from the La Mesa burn may enhance understanding of differences in winter range qualities and the potential impact of these differences on the elk population.

The overall purpose of the project was to examine the relationship between winter diet quality and animal condition in the Jemez Mountain elk. Specific objectives of my study were:

1. To determine diet composition of elk occupying burned and unburned winter ranges.
2. To measure nutritional value of elk forage species in the 2 winter ranges.

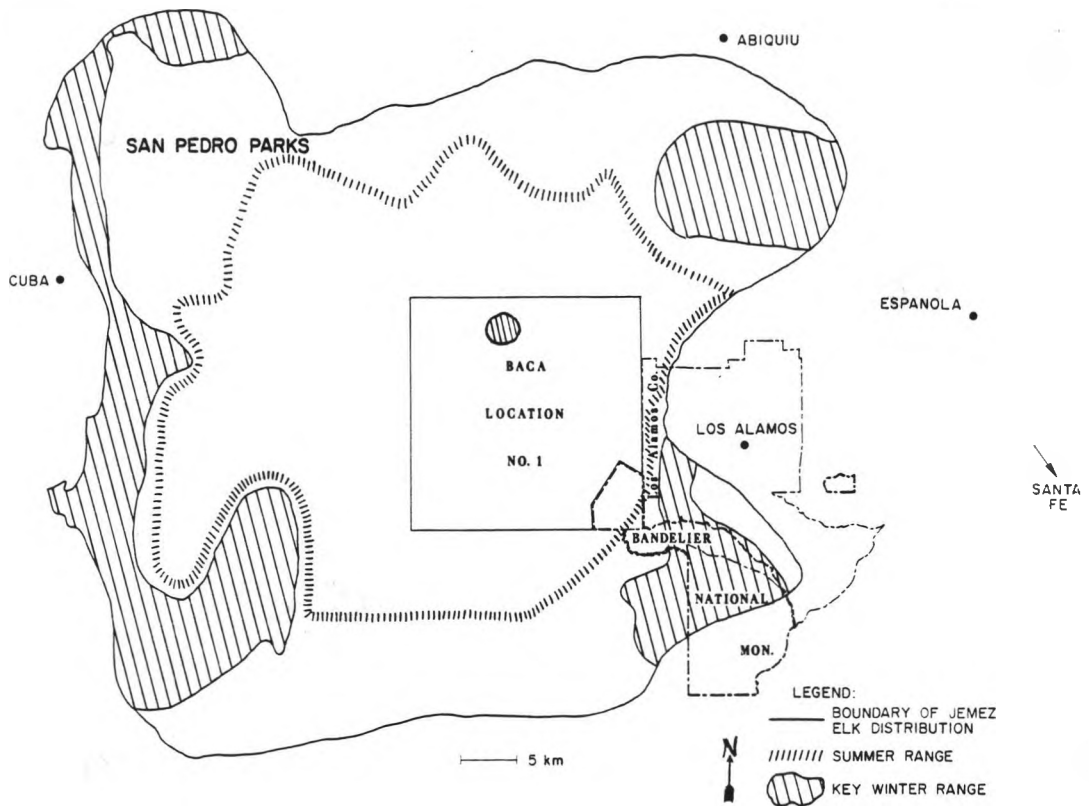


Figure 1. Distribution of elk in the Jemez Mountains, north-central New Mexico (updated from New Mexico Department of Game and Fish files, Santa Fe, 1980).

3. To estimate winter diet quality of elk using the 2 winter ranges.
4. To predict, through simulation modeling, effects of differences in diet quality on nutritional status of elk in the 2 areas.

Hypotheses addressed in the study are outlined in Table 1.

In a related study, blood sera, pregnancy determinations, and several length-weight measurements of trapped elk provided condition indices for animals in the study areas (Weber 1981). Trapped elk were also radio-collared to determine movements and degrees of association among elk from the 2 herds.

Table 1. Hypotheses addressed in study of winter diets of elk in the Jemez Mountains, New Mexico, 1980.

Hypothesis	Source	Test Criterion
1. Diets of elk from the La Mesa burn will contain more grass than will diets from the unburned area.	Kufeld 1973, Leege et al. 1977, Potter and Foxx 1979	Fecal samples from elk wintering in the 2 areas will be analyzed microhistologically.
2. Forage quality will be superior on the La Mesa burn.	Dewitt and Derby 1955, Vlamis and Gowans 1957, Duvall 1970, Hallisey and Wood 1976, Meneely 1978	Elk forage species from both areas will be analyzed for % crude protein and % digestible organic matter.
3. Grasses will increase in quality with advancing season, whereas browse quality will remain relatively constant.	Cook and Harris 1950, Dietz 1967, Burzlaff 1971, Hobbs et al. 1981	Changes in digestibility and crude protein content of grasses and browse will be statistically analyzed.
4. Elk diets from the La Mesa burn will be nutritionally superior to diets from the unburned area.	Einarson 1946, Duvall and Whitaker 1964, Leege 1969, Anderson et al. 1970, Lowe 1971, Smith and Owensby 1973	Products of diet botanical composition (%) x forage quality will be summed to estimate dietary protein and digestibility in both areas.

STUDY AREA

Study areas were located in Sandoval and Los Alamos Counties in north-central New Mexico (Fig. 2). In June 1977 the La Mesa conflagration burned approximately 6200 ha on the Pajarito Plateau 13 km south of Los Alamos, between the Jemez Mountains to the west and the Rio Grande valley eastward. Elevation of the burned area ranges from 2100 to 2460 m. Portions of Los Alamos National Laboratory (LANL), Sante Fe National Forest (SFNF), and Bandelier National Monument (BNM) were burned. In this study field investigations on the burn were conducted on BNM, hereafter referred to as "the burned area" or "Bandelier." A second elk wintering area selected for comparison was located on the northern perimeter of the Jemez Mountains in the Valle San Antonio at elevations of 2590 to 3180 m (Fig. 2). This area, which has not burned for at least 20 years, is part of a 56,000 ha ranch owned by the Baca Land and Cattle Company.

Existing geologic formations in the study areas were produced by sedimentation and extreme volcanism (USERDA undated). A series of eruptions 1.1-1.4 million years created the Valles Caldera, a basin-like formation 20-25 km wide and 150-600 m deep. The caldera is surrounded by and interspersed with peaks, thus forming the Jemez Mountains. Broad grassy valleys and wooded hillsides characterize the Jemez range. Slope ranges from 0-5% in valley floors to 80% on mountainsides.

Deposition of volcanic debris and ash flows along the flanks of the volcanic pile formed the Pajarito Plateau, extending south and east from the Jemez Mountains. The plateau is deeply dissected by

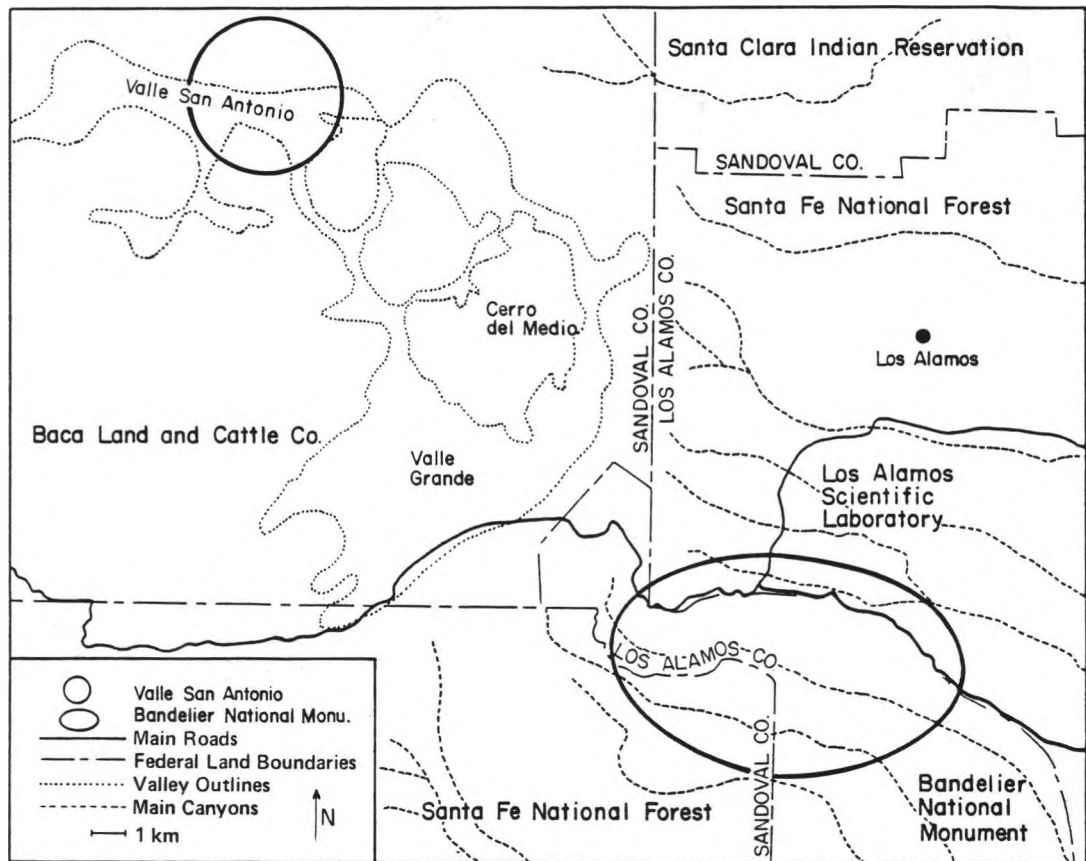


Figure 2. Location of study areas in the Jemez Mountains and Pajarito Plateau, north-central New Mexico.

precipitous canyons up to 200 m deep, with intervening mesas sloping gently southeastward. Slopes greater than 20% are most common in the plateau, although mesa tops average 0-5% slope. Soils in both areas are derived primarily from rhyolite and tuff (Nyhan et al. 1978).

Climate in the study areas is semi-arid, mountain continental. In the vicinity of Los Alamos, annual precipitation averages 45 cm, of which 75% occurs in July and August (Foxx and Potter 1978). Lower elevations near the Rio Grande may receive as little as 20 cm annually, whereas precipitation in the Valle San Antonio averages 60 cm annually (D. Swanson, USDA Soil Conservation Service, unpubl. data). An average of 125 cm snowfall, 200 cm at higher elevations, constitutes most winter precipitation. In Los Alamos average daily maximum and minimum temperatures for the year are 15.4 and 2.3 C, respectively (USERDA undated). An average of 150 days per year are frost-free in the Los Alamos area (Nyhan et al. 1978), compared with 70-100 days in the Valle San Antonio (D. Swanson, unpubl. data).

An elevational increase of 1500 m from the Rio Grande valley to the Jemez peaks creates a mosaic of vegetation types. Pinyon-juniper stands of the *Pinus ^{edulis} cembroides* Province (Daubenmire 1978) are common below 2300 m on the burn, with representative understory species including bottlebrush squirreltail, mountain muhly, true mountainmahogany, and wavyleaf oak.

Vegetation of the *Pinus ponderosa* Province dominates in the burned area, with ponderosa pine forming dense stands. Common shrubs include Gambel oak, New Mexico locust, and Fendler ceanothus. Associated grasses, typical of the province, are *Agropyron*, *Bouteloua*, *Festuca*,

Muhlenbergia, and *Poa* species. Of special interest was the seeding of 6 species of native grasses following the La Mesa fire, which produced dense swards (Potter and Foxx 1979). Seeded species included spike muhly, blue grama, sand dropseed, bluestem wheatgrass, slender wheatgrass, and sheep fescue. The last 2 species were most successfully established, primarily in severely burned sites (Potter and Foxx 1979, Appendix B). Several herbaceous species in the burned area exhibited gigantism (Foxx and Potter 1978), a typical occurrence following fires. Higher elevations and north-facing slopes in Bandelier support primarily mixed conifer communities of the *Pseudotsuga menziesii* Province. Dominant tree species are ponderosa pine, limber pine, Douglas-fir, and white fir, with scattered stands of aspen in more moist habitats and disturbed areas.

In the Valle San Antonio, mixed conifers prevail. However, south-facing slopes are largely composed of ponderosa pine and Gambel oak. Bunchgrasses, especially fescues, form a dense ground cover on these slopes. Other common grasses include mountain muhly, slender wheatgrass, and bluegrasses. Additional vegetation types present in the Valle San Antonio are wet meadows, dominated by sedges and bluegrasses, and subalpine forests of white fir, subalpine fir, blue spruce, and scattered Engelmann spruce.

Fire has been a major force in creating and maintaining ponderosa pine forests in a lightning bioclimate in the Southwest (Weaver 1967, Biswell 1972, Foxx and Potter 1978). Core sampling of pines for fire scars in Bandelier revealed an average fire frequency of 14 years for the pre-fire suppression period from 1777-1907 (Foxx and Potter 1978). An average of 6 fires per year occurred in the monument from 1931-1977,

of which only 6 consumed more than 4 ha (Foxx and Potter 1978). In the adjacent Sante Fe National Forest, an average of 1 lightning-caused fire per 400 ha occurred from 1945-1966 (Foxx and Potter 1978). Thus, fire has continued to modify the arid communities of the Jemez Mountains, despite over 50 years of attempted fire suppression.

Large mammals are an important esthetic and economic resource in the Jemez. Rocky Mountain mule deer (*Odocoileus hemionus*), year-round residents in Bandelier, also summer higher in the Jemez Mountains, including the Valle San Antonio. Feral burros (*Equus asinus*) inhabit lower elevations of Bandelier, but do not generally occupy ranges used by elk. Approximately 4000 cattle were grazed in summer 1979 on the Baca ranch (560 km²), including the study area. Bandelier lands have not been grazed by livestock since the monument's inception in 1916, excepting light grazing by caretaker's stock in the 1920s and 1930s (W. Sweetland, pers. commun.).

By the early 1900s, Rocky Mountain elk were virtually eliminated from the Jemez by market hunting and poaching (Gates 1967). Reintroduction commenced in 1948 with 28 animals from Jackson Hole, Wyoming (Lang 1958). The most recent transplants occurred in Los Alamos County in 1964-1965 when 58 Jackson Hole elk were released. Since 1965, elk have become established throughout the Jemez Mountains.

Approximately 200-400 elk wintered on 2000 ha in the burned area in 1979-1980. The number of elk wintering in the Valle San Antonio is estimated to be 50-100 animals. The majority of the population summers in the upper reaches of the mountains. Cerro del Medio, a peak in the southeastern quadrant of the caldera, has been identified as a major calving ground (White 1981).

METHODS

Diet Composition

Botanical composition of elk winter diets in the 2 study areas was determined by microhistological analyses of feces. This technique allows identification of forage taxa from cutinized plant epidermal fragments and lignified cell walls remaining after digestion (Dearden 1973, Dearden et al. 1975, Hansen et al. 1977). Fecal material was analyzed by the Composition Analysis Laboratory, Colorado State University, Fort Collins. To assist in forage identifications, plant samples were pressed, dried, and submitted to the lab as voucher specimens (Appendix A).

Fresh elk pellets were collected biweekly for 6 sampling periods, from 22 January to 11 April 1980, in both study areas. An additional collection period in Bandelier extended sampling there until 22 April. Sampling areas were those where elk were currently active, including feeding, bedding, and traveling sites. Sample size (number of pellet groups collected) within each biweekly period ranged from 14-44 in Bandelier and from 8-50 in the Valle San Antonio. At least 5 pellets were collected from each fresh group and preserved in table salt. One pellet from each group was removed to form a composite sample for each collection period in each area. Pellets were also obtained during February-April 1980 from 35 elk trapped in a related study (Weber 1981) and from 5 cow elk collected on the burn. One pellet from each animal was added to the appropriate composite sample; the remaining material was analyzed for each animal.

Pellets were washed and ground over a 1 mm screen. Twenty fields were read on each of 5 microscope slides prepared from each composite, totaling 100 fields read per composite. Only 1 slide (i.e. 20 fields) was read for each sample from the 40 elk of known sex and age. Results were reported in percent relative densities, which are highly correlated with percent composition of species mixtures on a dry weight basis (Sparks and Malechek 1968, Dearden et al. 1975). Plant fragments were identified to genera; however, some genera were represented in the study area by only 1 species and are reported as species.

Forage and Diet Quality

Approximately 200 elk pellets (1 pellet per group) were collected in fall 1979 on Bandelier, representing previous winter use of the burn. Analysis of this composite sample, coupled with feeding site examination in both study areas, indicated plants likely to be major elk forage species. These plants were collected biweekly in feeding sites in both areas, concomitant with fecal collections. Plant parts collected were dictated by observations of elk use, e.g. primarily basal leaves of grasses and only current annual growth or less of browse species were clipped. One hundred g of plant material, from at least 5 plants, were collected per species for each biweekly sample. Samples were collected from plants that had been previously grazed or browsed or were adjacent to such plants. Forages were frozen within 10 h of collection.

Results of fecal analyses determined those species requiring nutritional analyses. Only samples of species occurring in the diet in the corresponding collection period, as inferred from fecal analysis, were

analyzed for forage quality comparisons. In some instances, a species was not collected in a period when it occurred in the diet, but was collected in other periods. For these species, all samples collected were analyzed, regardless of occurrence in the diet. Missing values were then predicted using regression analysis; these values were used in subsequent diet quality calculations.

Samples were dried at 55 C in a forced-air oven and ground in a Wiley mill using a 1 mm mesh screen. Subsamples were dried at 100 C to determine percent dry matter. Percent organic matter was calculated following ashing of subsamples in a muffle furnace at 600 C for 5 h. Crude protein (Kjehldahl N x 6.25) was determined for all samples following AOAC (1965) procedures and was expressed on an organic matter basis. Dry matter, ash, and nitrogen percentages were determined by technicians at the Natural Resource Ecology Laboratory, Colorado State University.

In vitro digestibility of each forage was determined in triplicate, using a modification of the 2-stage technique described by Tilley and Terry (1963) and Pearson (1970). Estimates of *in vitro* digestibilities from this technique are highly correlated with *in vivo* forage digestibilities (Scales et al. 1974, Milchunas et al. 1978, Palmer and Cowan 1980). All samples were digested in 1 run, as suggested by Tilley and Terry (1963), thereby eliminating potential between-run variation. Digestibility of 5 standard forages included in the run did not differ significantly from their known values ($P > 0.70$). Ten blanks were included to account for fibrous material and microorganisms in the inoculum. Rumen fluid was vacuum-pumped from a fistulated cow fed a native winter hay diet for more than 2 weeks prior to fluid collection. Feed was removed 12 h and

water 4 h before vacuum-pumping. Following termination of *in vitro* digestion, residues were vacuum-filtered using fiberglass filters, dried at 100 C, cooled, and weighed. Residues were subsequently ashed at 600 C to obtain organic matter digestibility coefficients, as recommended by Milchunas et al. (1978) and Alexander and McGowan (1966). Ten filters were also ignited to account for filter ash in residues. The formula for calculation of *in vitro* digestible organic matter (IVDOM) was as follows:

$$\text{IVDOM} = \text{sample wt} \times \text{OM\%} - (\text{residue} - \text{blank} - \text{filter} - (\text{residue ash} - \text{blank ash} - \text{filter ash})) / \text{sample wt} \times \text{OM\%}.$$

Diet composition percentages from composite samples were normalized to total 100, as all taxa identified in fecal analyses were not analyzed for forage quality. Normalized diet percentages were multiplied by crude protein and IVDOM coefficients for the appropriate species; these products were summed within each period to obtain dietary protein and digestibility in each area. Diet quality values were similarly calculated for elk from which fecal samples were collected directly.

Simulation of Elk Nutritional Status

A simulation model of ruminant energy and nitrogen balance (Swift 1978) was used to assess potential effects of differences in diet quality on winter nutritional status of elk in the 2 herds studied. Hobbs (1979) and Carpenter and Torbit (1980) have used the model to simulate condition in elk and mule deer, respectively. The model is a difference equation model that operates at single day time steps. It is divided into 3 submodels: energy, nitrogen, and rumen microbe flow

(Fig. 3). Model objectives are prediction of forage intake rates, rates of digestion and metabolism of energy and nitrogen, partitioning of energy and nitrogen within the body, and losses from the body of energy and nitrogen. The model operates on an individual animal basis. Model output includes body weight, partitioned into lean body and fat components, and total energy and nitrogen balance.

To examine effects of diet quality differences between the 2 areas, elk condition was studied using the model over a 14-week period, beginning 22 January. The model was initiated on day 1 with a hypothetical 590-day old elk weighing 215 kg. One simulation was made for each area, with input of corresponding weather data, diet nitrogen, and diet digestibility. Therefore, all parameters except meteorological data and diet quality were equal in the 2 runs. Weather data input consisted of daily maximum and minimum temperatures. Records were obtained from Bandelier National Monument and a Department of Energy weather station at Fenton Hill, approximately 16 km southwest of the Valle San Antonio at an elevation of 2710 m. Diet quality data were input 7 times in Bandelier and 6 times in the Valle San Antonio runs, corresponding with mid-points of collection periods.

Statistical Analysis

Diet composition, determined from composite and individual fecal samples, was analyzed using multivariable analysis of variance. Temporal changes in diet composition of individual elk were described using simple linear regression analysis. In Bandelier, where results from 6 collection periods were available for comparison, differences in diet estimations using composite and individual samples were tested with a paired Student's t-test.

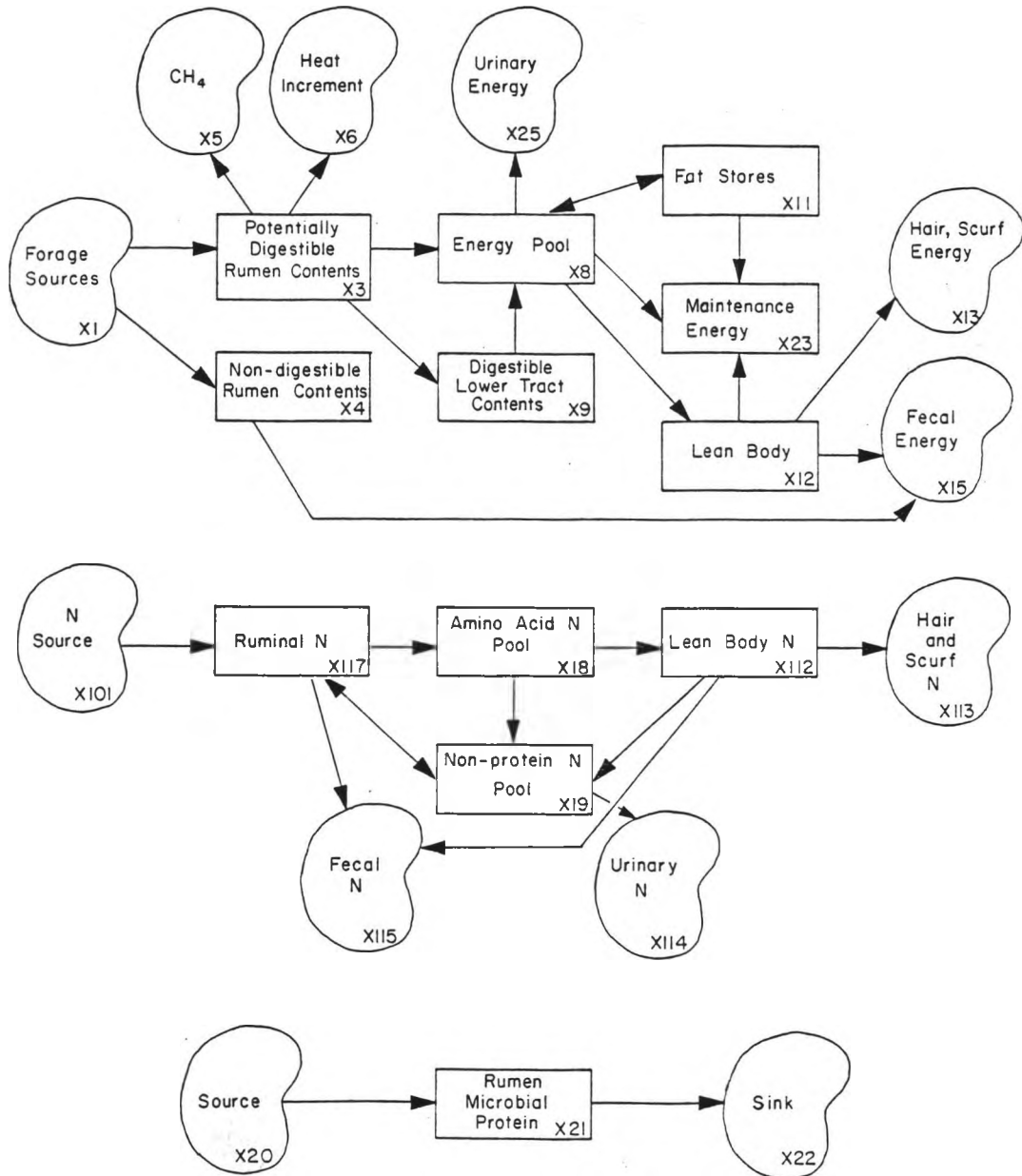


Figure 3. Structure of ruminant energy and nitrogen balance model used in simulation of elk nutritional status (from Swift 1978).

Variability in crude protein and IVDOM among forage classes (i.e. grasses, forbs, and shrubs) and between locations was analyzed with analysis of variance. Stepwise polynomial regression and analysis of variance were used to examine changes in forage quality with time.

Diet quality data were obtained using both composite and individual fecal samples. Observations available from composite samples, totaling 6 for each area, were compared using a paired t-test and multiple regression analysis with dummy variables. All statistical tests were performed at the 95% confidence level. Regression analyses and analysis of variance were conducted using SPSS (Statistical Package for the Social Sciences, Nie et al. 1975).

Evaluation of diet quality differences among elk related to sex, age, location, and time was difficult because not all age classes, nor both sexes, were captured in all time periods; consequently, sample sizes were not equal among periods. Therefore, a modified analysis of variance was used that provided least-squares estimates for missing values (W. Harvey and C. Gaskin, unpubl. rep., Colo. State Univ. Stat. Lab., Ft. Collins, Colo., 1974). Because only 3 elk (all from Bandelier) were trapped prior to period 4, these samples were not included in subsequent analysis. In addition, forage samples were not collected in period 7 in the Valle San Antonio, although 2 elk were trapped there during that time. Regression analysis provided estimates for diet protein, but diet digestibility for these animals could not be predicted from regression.

Subsets of the factorial model were used to assess age and sex effects, using an iterative approach. First, a full model, with values

for all individuals was used. Subsequent analyses were made with only a subset of the original data, e.g. males or calves excluded, depending on the effect under consideration. When models were selected on the basis of sex, the analysis of variance included age, time, and location, but not sex, as factors. Location x time interactions were compared among models to evaluate effects due to elimination of some sex or age class. Thus, differences due to sex were assessed using sex as a factor in the runs in which models were based on age classes, as well as by direct comparison of location x time interactions of models based on sex. Age effects were evaluated similarly. Differences among means were tested with Tukey's Q (Kleinbaum and Kupper 1978).

RESULTS

Diet Composition

Composite samples. Diets of elk in the 2 study areas contained markedly different proportions of graminoids (includes grasses and grass-like plants) and browse; grasses, however, dominated both diets (Table 2, Fig. 4). Elk on the burned area consistently consumed large amounts of grasses, which averaged 90% of the diet (range = 83-98% among periods). In contrast, consumption of grass by elk in the Valle San Antonio was significantly less ($P < 0.001$), averaging only 52% (range = 48-57%). Browse constituted a substantial proportion of the diet in the Valle San Antonio ($\bar{x} = 41\%$), but was eaten in much lower quantities in Bandelier ($\bar{x} = 4\%$, $P < 0.001$). Forbs were a uniformly minor dietary component and were consumed equally in the 2 areas ($P > 0.90$). Composition of elk diets did not change significantly through the winter and early spring in either location ($P > 0.30$, Fig. 4).

Two taxa, *Agropyron* and *Festuca*, constituted 80% of the diet in Bandelier, resulting in a singularly uniform diet. Presumably most of this consumption was of slender wheatgrass and sheep fescue, which are ubiquitous on the burn as a result of reseeding (Potter and Foxx 1978). Fescue alone accounted for 70% of the diet in Bandelier, and its occurrence in the diet was the least variable of all taxa in this study ($CV = 10\%$). Other important grasses in the diet were prairie junegrass and bluegrasses. A maximum of 4 grasses contributed 2% or more to the diet in any collection period in Bandelier.

Table 2. Mean percent relative density of major forage species identified in elk fecal material, January-April 1980, in the Jemez Mountains, north-central New Mexico.^a

Taxon ^b	Bandelier National Monument			Valle San Antonio		
	\bar{x} (%)	SD	CV ^c (%)	\bar{x} (%)	SD	CV (%)
Graminoids^d						
<i>Agropyron</i> spp.	9.2	4.2	46	8.1	2.3	28
<i>Bromus</i> spp.				1.0	1.5	150
<i>Carex</i> spp.	1.1	0.8	73	6.7	4.2	63
<i>Danthonia</i> spp.				2.0	2.0	100
<i>Deschampsia caespitosa</i>	1.2	1.0	83	1.0	1.0	100
<i>Festuca</i> spp.	70.8	6.8	10	27.1	6.7	25
<i>Koeleria cristata</i>	3.3	2.1	64	1.4	1.0	71
<i>Poa</i> spp.	2.6	2.3	88	2.4	1.7	71
<i>Sitanion hystrix</i>	0.6	0.8	133			
Total graminoids ^e	90.1	4.7	5	52.2	3.2	6
Browse						
<i>Berberis</i> spp.				5.3	4.3	81
<i>Juniperus</i> spp.				0.6	1.2	200
<i>Picea pungens</i>	1.6	1.1	69	9.4	4.7	50
<i>Potentilla</i> spp.				1.1	1.6	145
<i>Pseudotsuga menziesii</i>				10.7	4.1	38
<i>Quercus</i> spp.				9.7	6.0	62
<i>Shepherdia</i> spp.				1.9	4.7	247
Total browse ^e	4.2	2.4	57	40.9	5.5	13
Forbs						
<i>Equisetum laevigatum</i>	1.4	0.8	57	2.6	2.1	81
Total forbs ^e	4.7	1.8	38	4.7	4.7	100
Unknown	1.0	1.0		2.2	1.2	

^aMean percentages calculated across 7 and 6 collection periods in Bandelier and the Valle San Antonio, respectively, using composite fecal samples.

^bIncludes those taxa comprising at least 2% of the diet in any collection period.

^cCoefficient of variation.

^dIncludes grasses and grasslike plants.

^eIncludes all taxa identified.

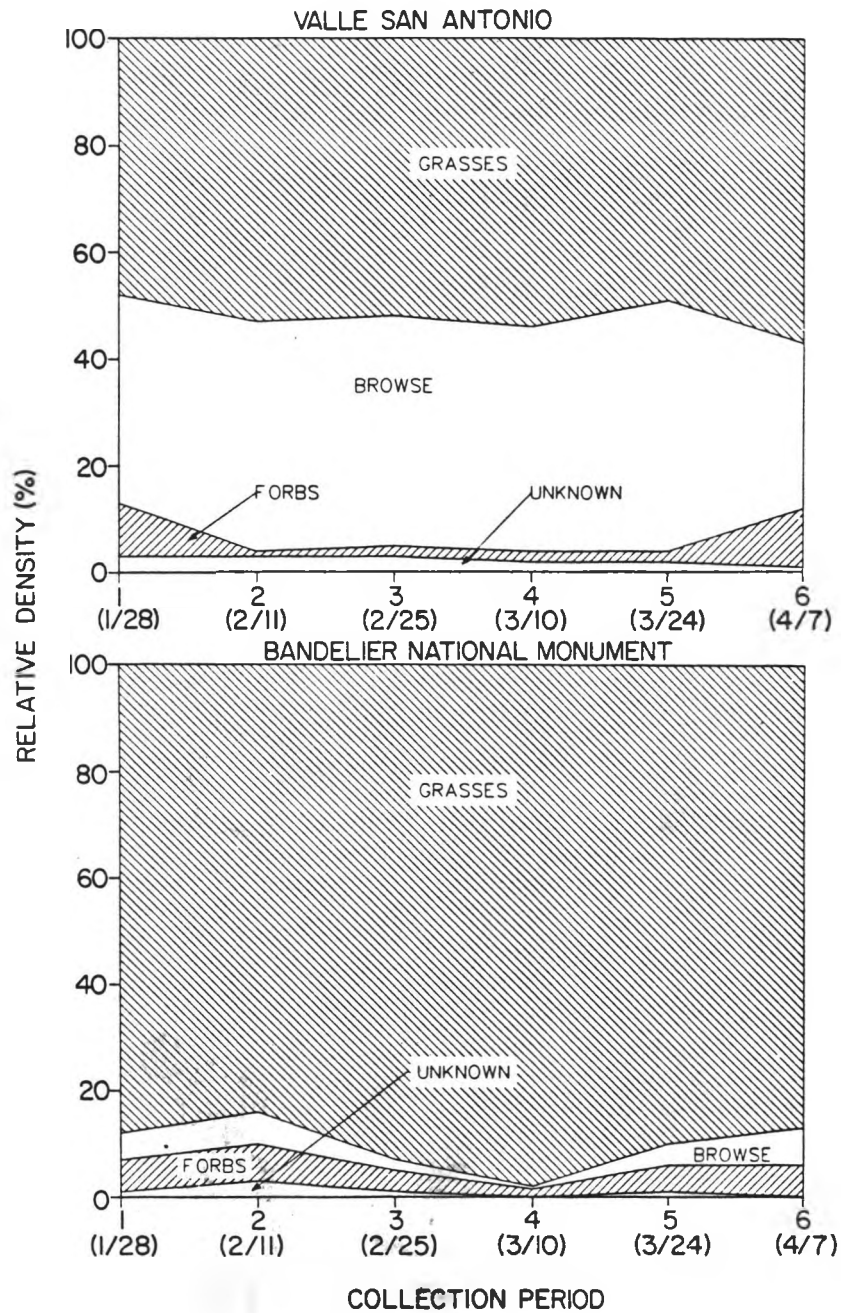


Figure 4. Botanical composition of elk winter diets, determined by micro-histological analysis of feces, in the Jemez Mountains, north-central New Mexico, 1980. Dates are mid-points of biweekly collection periods.

Blue spruce was the only woody plant consumed in more than trace amounts in Bandelier. Although evidence of browsing on Gambel oak, Douglas-fir, aspen, and true mountainmahogany was often observed, mule deer also wintered on the burn, and no distinction between browsing by the 2 cervids could be made.

In the Valle San Antonio, 8 taxa constituted 80% of the diet; thus, elk diets in this location were more diverse than in Bandelier (Table 2). Fescues were dominant, as in the burned area, averaging 27% of the diet. Arizona and Thurber fescues were especially common in the Valle San Antonio, forming a thick mat over many south-facing slopes. Evidence of consistent grazing of Arizona fescue was observed throughout winter. Other graminoids consumed included wheatgrasses, sedges, and bluegrasses. Smooth horsetail was the only forb consumed regularly in this area.

Browse species were an important dietary component in the Valle San Antonio. The 3 major species, totaling 30% of the diet, were Douglas-fir, Gambel oak, and blue spruce. Creeping mahonia was also a regular diet item. Aspen appeared in only trace amounts in the feces analyzed, although browsing of twigs and bark was observed throughout the Valle San Antonio.

Individual samples. Pellets from captured and collected elk were analyzed to examine differences in diet composition due to location, sex, and age. Percentages of grasses and browse consumed were significantly different between study areas ($P < 0.001$, Table 3), corroborating results from analysis of composite samples. Forbs averaged less than 2% of the diet in both areas. Hence, although many differences in forb consumption among locations, sexes, and ages were statistically significant, these differences were of little biological importance. Because of their minor

Table 3. Diet composition, determined by microhistological analysis of feces, of captured and collected elk in the Jemez Mountains, north-central New Mexico, during February-April 1980.

Age	Bandelier National Monument					Valle San Antonio				
	% Grass		% Browse		N	% Grass		% Browse		N
	\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD	
Calf										
2/26 ^a	97 ^b	0	0	0	1					
3/25	98	1	3	1	2	23	18	77	18	3
Total	97	1	2	2	3	23	18	77	18	3
Yearling										
2/12	94	0	2	0	1					
3/11	98	3	2	3	4	20	0	80	0	1
3/25	84	2	15	4	2	13	1	85	1	2
4/8	98	0	2	0	1	71	9	29	9	2
4/22	100	0	0	0	1					
Total	95	6	5	6	9	38	31	62	30	5
Adult										
2/26	87	0	7	0	1					
3/11	96	7	3	6	4	41	0	59	0	1
3/25	95	4	3	2	3					
4/8	91	4	9	4	2	69	13	31	13	5
4/22	98	1	2	1	2	82	14	18	14	2
Total	95	5	4	4	12	69	17	31	17	8
TOTAL	95	5	4	5	24	50	28	50	28	16

^aMid-points of biweekly sampling periods.

^bExpressed as % relative density of identified fragments.

contribution to elk diets in this study, forbs were not considered in subsequent diet composition and forage quality analyses.

Male and female elk selected similar diets in this study. In Bandelier, age had little influence on diet composition, but in the Valle San Antonio, calves consumed more browse and less grass than did older animals (Table 3). However, this difference among age classes was confounded with temporal changes in diet composition. Both yearling and adult elk consumed increasingly more grass and less browse with advancing season in the Valle San Antonio (Table 3). Analysis of composite samples also revealed a slight increase in grass consumption in the final period (Fig. 4). Seven of 8 adults in the Valle San Antonio were captured during the last 2 periods, potentially inflating differences in diet composition among age classes. Calves were trapped only during the 1 period when adults were not captured in the Valle San Antonio, rendering direct comparison infeasible. Thus, with no further evidence, diet composition differences among age classes cannot be considered biologically significant.

Analysis of individual fecal samples yielded results similar to those of composite samples in Bandelier (Fig. 5; $P > 0.05$, grasses; $P > 0.70$, browse). Only 3 periods were available for comparison between sampling methods in the Valle San Antonio; hence, no statistical tests were performed. Differences between diet estimates were not consistent among periods (Fig. 6). This inconsistency diminished in period 6 with the increase in grass and concomitant decrease in browse in samples from handled elk. The peak grass consumption, as determined by analysis of composite samples, occurred in the final collection period. Whether

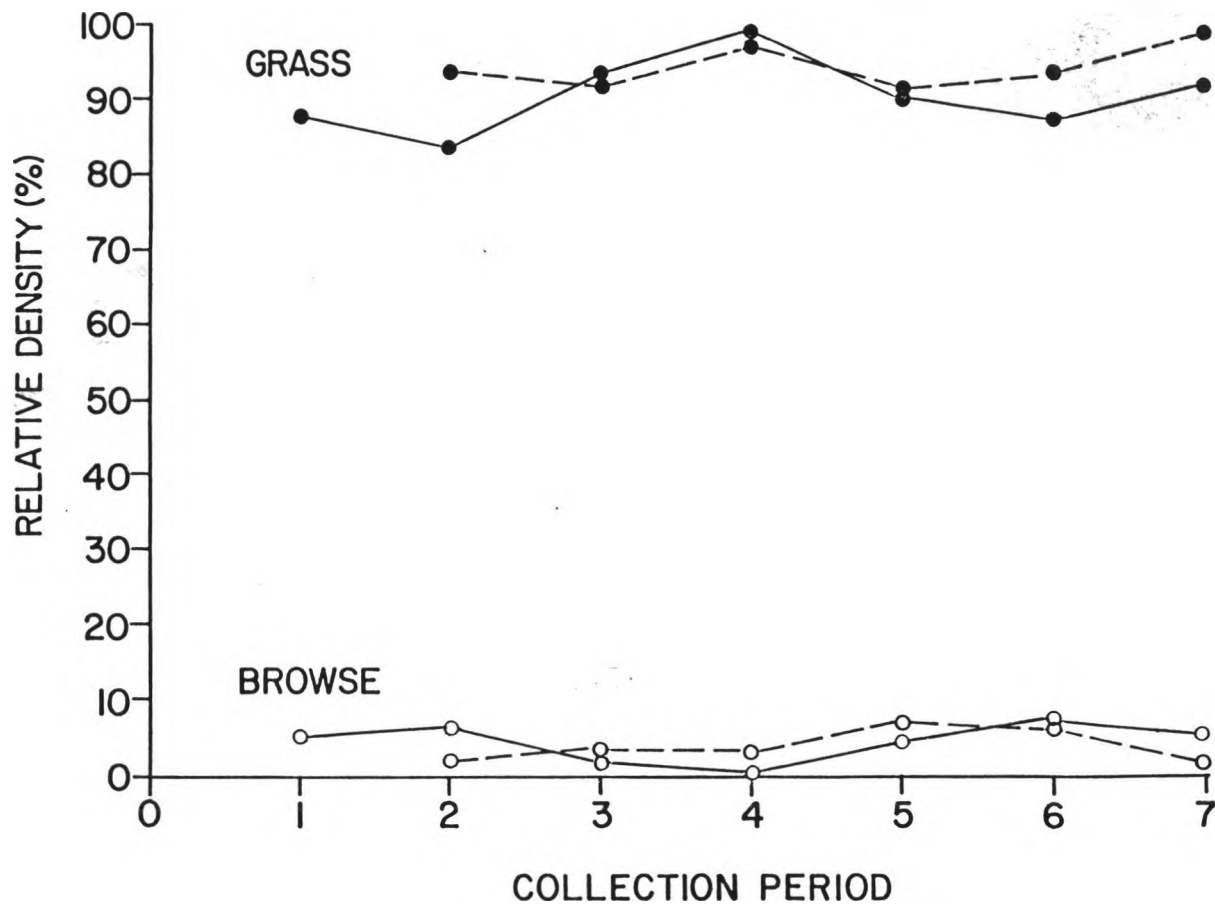


Figure 5. Diet composition of elk in Bandelier National Monument, New Mexico, January-April 1980, determined by microhistological analysis of composite and individual pellet group samples. Dashed lines represent individual samples; solid lines are composite samples. Data for composite samples are single observations; data for individual samples are means across animals. See Fig. 4 for dates of collection periods.

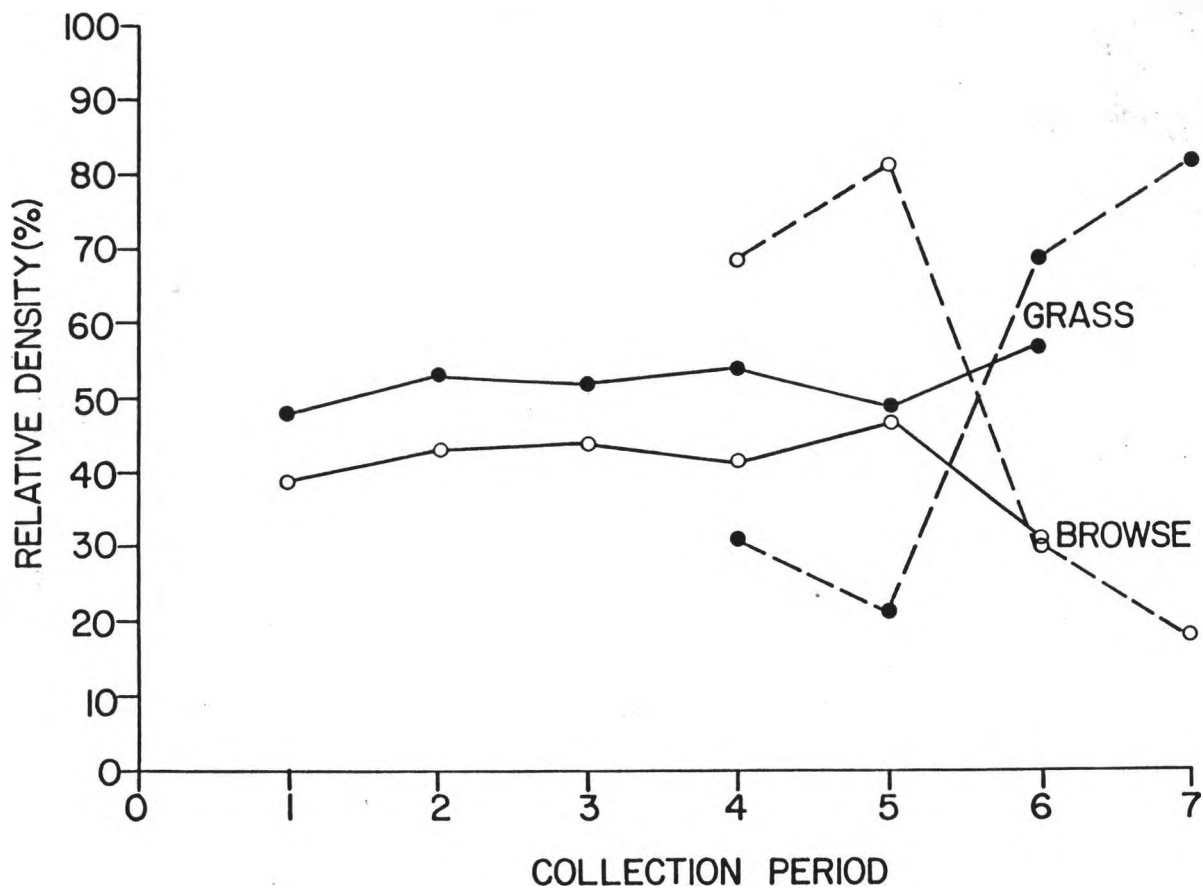


Figure 6. Diet composition of elk in the Valle San Antonio, New Mexico, January-April 1980, determined by microhistological analysis of composite and individual pellet group samples. Dashed lines represent individual samples; solid lines are composite samples. Data for composite samples are single observations; data for individual samples are means across animals. See Fig. 4 for dates of collection periods.

this increase would have continued to parallel that observed in individual samples from periods 6-7 is unknown.

Ranks of major forage species determined with individual samples were similar to ranks from composite samples (Table 4). In Bandelier, *Festuca* and *Agropyron* were the 2 primary taxa, confirming results from composite samples. Minor species, constituting no more than 5% of the diet, were not ranked similarly between collection techniques. The order of the 2 primary forages was reversed in the Valle San Antonio (Table 4). In general, ranks of other important forage species were similar. Notable differences were the absence of *Stipa* in the composite samples and the relative unimportance of *Agropyron* in the individual samples. However, these taxa were both less than 10% of the diets. Diets estimated from composite samples were more diverse than those from individual samples, i.e. more species accounted for 1% or more of the diet in composite samples (Table 4).

Summary. Elk in Bandelier consumed significantly more grass than elk in the Valle San Antonio; reseeded grasses constituted over 80% of the diet on the burn. In the Valle San Antonio, where diets were more diverse, grasses and browse were consumed in nearly equal proportions. Forbs were only minor diet items in both areas. Diet botanical composition did not change during the winter and early spring, and no differences in diets were observed among sex and age classes of elk. Results from composite vs. individual fecal samples were generally similar.

Table 4. Ranks of forages contributing at least 1% to elk diets in the Jemez Mountains, January-April 1980, determined by microhistological analysis of individual and composite fecal samples.

Rank	Bandelier National Monument ^a		Valle San Antonio	
	Individual	Composite	Individual	Composite
1	<i>Festuca</i> spp.	<i>Festuca</i> spp.	<i>Pseudotsuga menziesii</i>	<i>Festuca</i> spp.
2	<i>Agropyron</i> spp.	<i>Agropyron</i> spp.	<i>Festuca</i> spp.	<i>Pseudotsuga menziesii</i>
3	<i>Carex</i> spp.	<i>Koeleria cristata</i>	<i>Picea pungens</i>	<i>Quercus gambelii</i>
4	<i>Picea pungens</i>	<i>Poa</i> spp.	<i>Quercus gambelii</i>	<i>Agropyron</i> spp.
5		<i>Picea pungens</i>	<i>Stipa</i> spp.	<i>Berberis</i> spp.
6		<i>Equisetum laevigatum</i>	<i>Carex</i> spp.	<i>Picea pungens</i>
7		<i>Deschampsia caespitosa</i>	<i>Pinus</i> spp.	<i>Carex</i> spp.
8		<i>Carex</i> spp.	<i>Berberis</i> spp.	<i>Poa</i> spp.
9			<i>Cercocarpus/Ceanothus</i> ^b spp.	<i>Danthonia</i> spp.
10				<i>Equisetum laevigatum</i>
11				<i>Koeleria cristata</i>
12				<i>Bromus</i> spp.
13				<i>Potentilla</i> spp.
14				<i>Muhlenbergia</i> spp.
15				<i>Deschampsia caespitosa</i>

^aRanks calculated from means of periods 2-7 in Bandelier and 4-6 in the Valle San Antonio.

^bThese genera cannot be separated in fecal analysis.

Forage Quality

Forage samples analyzed were those contributing to elk diets in the periods sampled. Therefore, forage quality comparisons relate only to forages identified in elk fecal material, rather than a comprehensive sampling of available species in the study areas.

Throughout the winter, grasses were more digestible than were browses ($P < 0.005$, Table 5). This difference was more pronounced in Bandelier, where digestibility of grasses was 13 percentage units greater; in the Valle San Antonio, the difference was only 5 units (units of digestibility and protein refer to percentage units). Of the 8 browse samples from Bandelier, 5 were Gambel oak twigs. Thus, comparisons in this area were essentially of 6 grass species with Gambel oak.

Although overall differences between forage classes in crude protein were not significant ($P > 0.65$, both locations), browse contained more protein than did grasses from January-March. With initiation of spring growth, however, grass protein increased and exceeded that in browse by April.

Browse forages were generally less variable in quality than were grasses. This consistency in browse quality may be explained in part by a relative lack of interspecific variation in quality among browse species and the absence of distinct temporal changes in browse quality during this study. Unlike woody species, grasses consumed by elk exhibited measurable changes in quality with advancing season (Figs. 7, 8), especially in Bandelier ($P < 0.001$, Bandelier; $P < 0.01$, Valle San Antonio). The regressions were curvilinear, with the exception of IVDOM in the Valle San Antonio.

Table 5. Crude protein and *in vitro* digestibility of elk forage species collected January-April 1980 in the Jemez Mountains, New Mexico.

Taxon	Bandelier National Monument					Valle San Antonio				
	IVDOM (%) ^a		Crude protein (%) ^b		N ^c	IVDOM (%)		Crude protein (%)		N
	\bar{x}	SE	\bar{x}	SE		\bar{x}	SE	\bar{x}	SE	
Graminoids^d										
<i>Agropyron trachycaulum</i>	39	4.0	5.2	1.2	7	31	1.8	3.8	0.7	4
<i>Bromus</i> spp.						31		2.8		1
<i>Carex</i> spp.	40	2.8	5.3	0.8	5	54	5.5	12.0	2.2	5
<i>Danthonia parryi</i>						28		2.4		1
<i>Deschampsia caespitosa</i>						29		4.5		1
<i>Festuca arizonica</i>						37	0.7	4.3	0.4	6
<i>Festuca ovina</i>	40	1.6	4.6	0.4	6					
<i>Juncus</i> spp.						31	1.5	6.2	0.7	2
<i>Koeleria cristata</i>	43	6.7	5.7	1.9	6	31	2.4	2.6	0.2	2
<i>Muhlenbergia montana</i>						29	1.1	3.5	0.7	3
<i>Poa</i> spp.	43	2.7	5.9	0.8	2	38	2.5	6.5	2.5	5
<i>Sitanion hystrix</i>	42	12.9	5.2	3.1	2					
\bar{x} , graminoids	41	1.9	5.3	0.5	28	37	1.8	5.7	0.8	30
Browse										
<i>Cercocarpus montanus</i> twigs	26		8.4		1					
<i>Juniperus communis</i> ^e						36		6.6		1
<i>Phoradendron</i> spp.						36	0.3	7.3	0.1	2
<i>Picea pungens</i> ^e						36	0.5	6.8	0.2	6
<i>Potentilla fruticosa</i> twigs						17		5.2		1
<i>Pseudotsuga menziesii</i> ^e	33		6.1		1	34	0.3	6.7	0.3	4
<i>Quercus gambelii</i> twigs	24	0.8	5.3	0.1	5	26	1.1	5.8	0.3	6
<i>Yucca</i> spp.	46		8.0		1					
\bar{x} , browse	28	2.9	6.1	0.5	8	32	1.3	6.4	0.2	20

^a*In vitro* digestible organic matter.

^bExpressed on organic matter basis.

^cNumber of samples.

^dIncludes grasses and grasslike plants.

^eTwigs and needles.

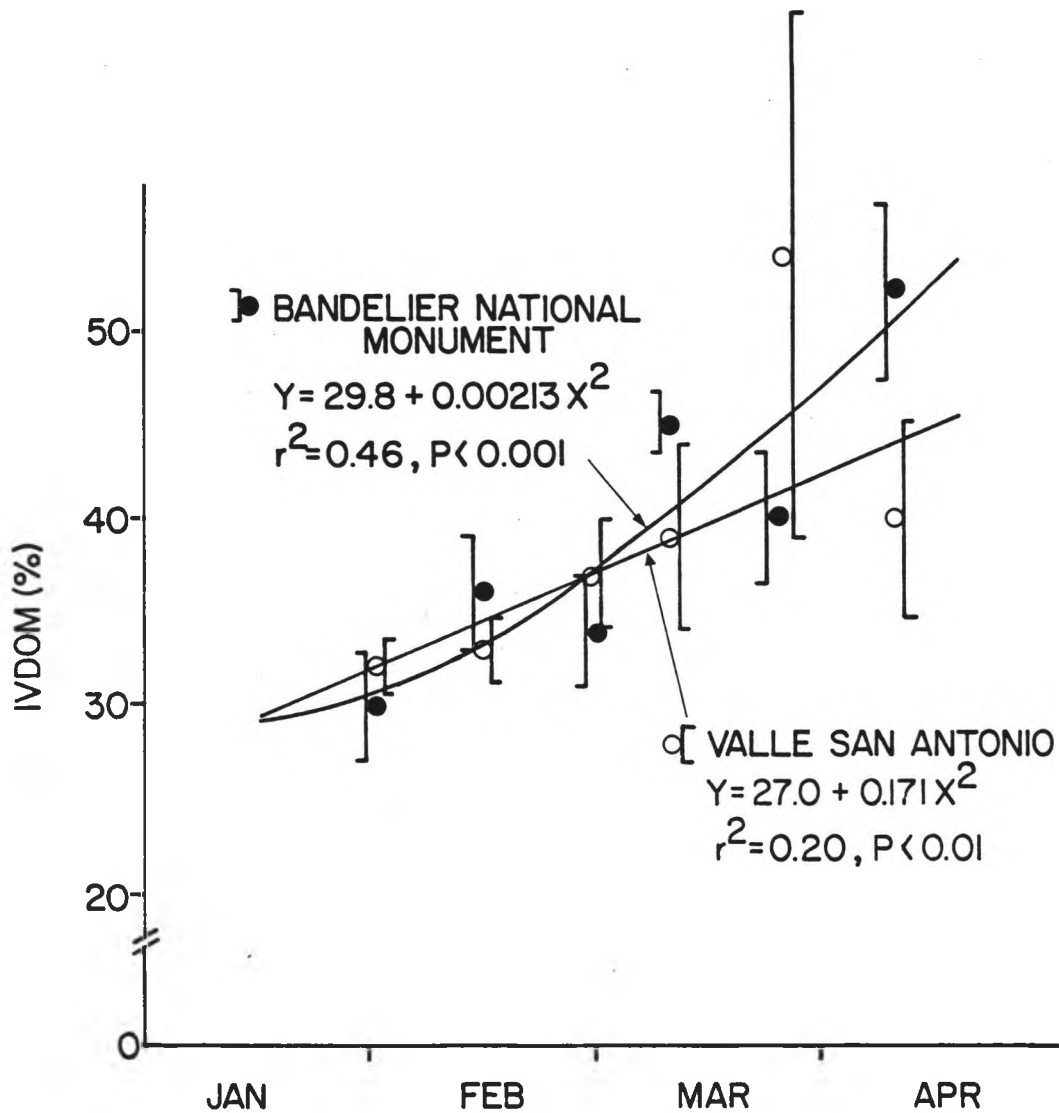


Figure 7. *In vitro* digestible organic matter ($\bar{x} \pm SE$) of grasses consumed by elk in the Jemez Mountains, north-central New Mexico, 1980. x = Julian calendar days.

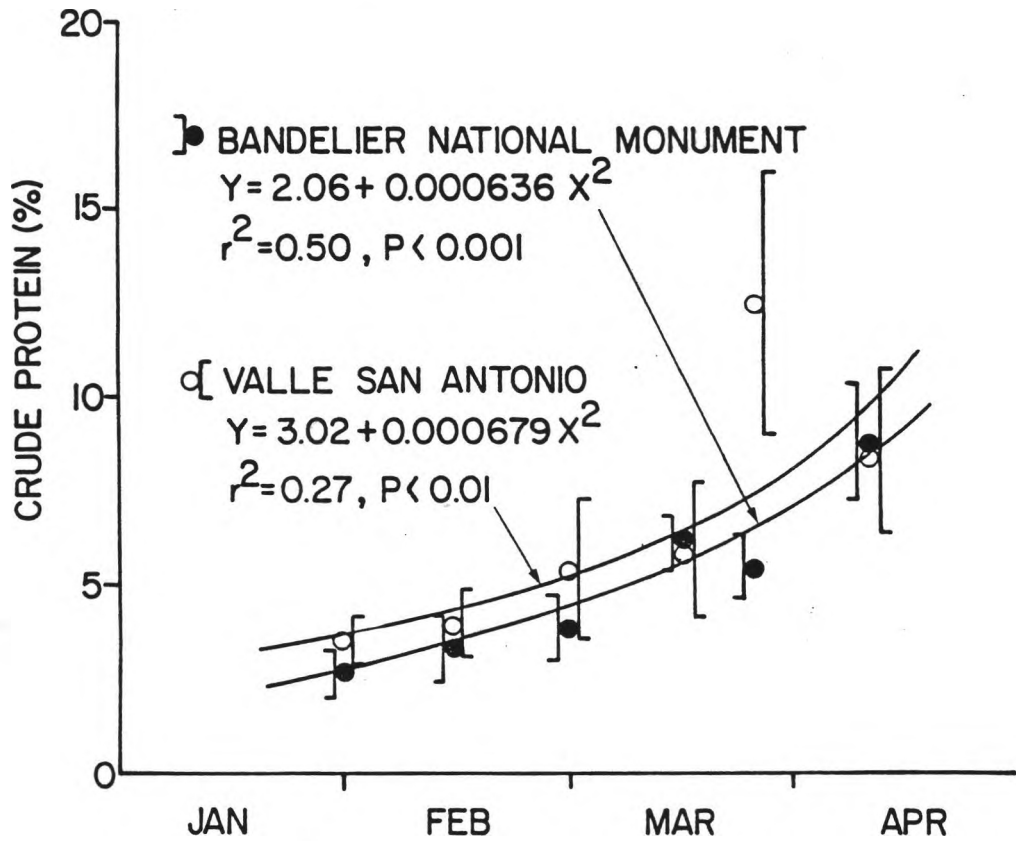


Figure 8. Crude protein ($\bar{x} \pm SE$), expressed as % organic matter, of grasses consumed by elk in the Jemez Mountains, north-central New Mexico, 1980. x = Julian calendar days.

In comparing forage quality between locations, samples collected in late April (period 7) in Bandelier were excluded from analysis, because no equivalent collections were made in the Valle San Antonio at this time. The quality of elk forages was exceptionally similar between areas (Table 5). For example, digestibility of grasses was only 4 units greater in Bandelier ($P>0.90$). This similarity between locations is particularly noteworthy considering the majority of grass samples from the Valle San Antonio (60%) were collected during the first half of the study, unlike in Bandelier (45%). This differential sampling intensity during a period of relatively low forage quality would be expected to inflate differences between locations; however, this was not the case. Mean protein in grasses and browse and IVDOM in browse were higher in the Valle San Antonio (Table 5), but not significantly ($P>0.05$).

Differences in forage quality between locations may have been influenced by dissimilar floristic compositions. Forages collected for analysis that were consumed by elk during the same periods in both areas included slender wheatgrass, prairie junegrass, and Gambel oak. Comparisons of these species with paired t-tests revealed no differences in protein or IVDOM between areas ($P>0.30$).

Ash content of elk forages was unusually large, averaging 11% in Bandelier and 7% in the Valle San Antonio. Whether this phenomenon was attributable to mineral content within plants or merely superficial adhesion is unknown. Graminoids contained especially large quantities of minerals, particularly slender wheatgrass and *Carex* spp. (\bar{x} = 16 and 15%, respectively). Sims et al. (1971) reported western wheatgrass,

which averaged 9% ash, to be a major contributor of minerals in eastern Colorado sandhills grasses. No seasonal trends in ash content were evident, a result also noted by Sims et al. (1971).

Summary. Grasses were generally more digestible than were browse species, but differences in protein were slight. Quality of grasses increased measurably with advancing season, whereas browse forages remained relatively constant in IVDOM and protein. Comparisons of forage quality between study areas revealed no significant difference in either grasses or browse.

Diet Quality

Composite samples. Elk diet quality differed among time periods as well as between locations. Increases in diet quality with advancing season reflected changes in quality of grasses, which were the major dietary components in both areas. Both browse quality and diet botanical composition remained relatively constant, and thus could not account for observed increases in diet quality.

Digestibility of elk diets in Bandelier exceeded that of the Valle San Antonio diets in 5 of 6 periods ($P < 0.05$, Table 6); mean diet IVDOM was 5 units higher in Bandelier. Differences in diet IVDOM between areas were related to differential temporal changes in diet digestibility (Fig. 9). Although diet IVDOM increased in both areas from January-April, the rate of increase was higher in Bandelier ($P < 0.05$). Elk diets in the 2 locations were of equal digestibility in January, but diet IVDOM was 10 units higher in Bandelier by mid-March. This marked difference persisted through the remainder of the study. From January

Table 6. Digestibility and protein content of winter diets of elk in the Jemez Mountains, north-central New Mexico, during January-April 1980.

Diet constituent	Date ^a							\bar{x}	SE
	1/29	2/12	2/26	3/11	3/25	4/8	4/22 ^b		
IVDOM ^c									
Bandelier National Monument	36	37	36	44	43	48	55	43	2.6
Valle San Antonio	33	35	37	34	36	39		36	1.0
Crude protein (% organic matter)									
Bandelier National Monument	3.5	3.5	4.1	5.8	5.7	7.2	8.0	5.4	0.7
Valle San Antonio	5.1	4.7	5.4	5.3	6.6	7.5		5.8	0.4

^aMid-points of biweekly sampling periods.

^bNo diet data collected in Valle San Antonio.

^c*In vitro* digestible organic matter.

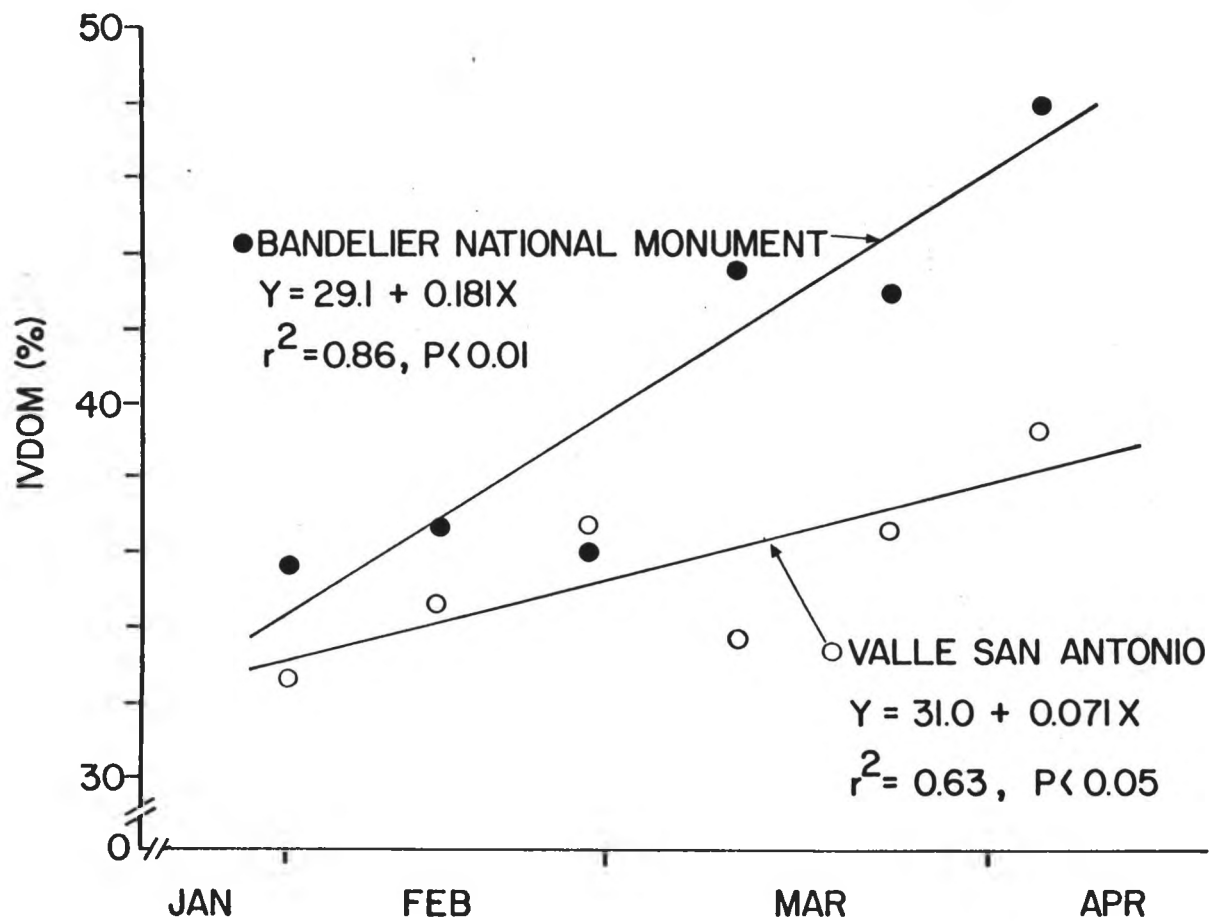


Figure 9. *In vitro* digestible organic matter in diets of elk in the Jemez Mountains, north-central New Mexico, 1980. x = Julian calendar days.

to April, diet digestibility increased 12 units in Bandelier, but only 6 units in the Valle San Antonio.

Differences in dietary protein between study areas were not as pronounced as were differences in diet digestibilities (Table 6). Mean diet protein was 0.8 units greater in the Valle San Antonio and in all but 1 period exceeded that in Bandelier ($P > 0.05$). Unlike diet IVDOM, diet protein differences were more substantial earlier in the year. Initial differences exceeded 1.5 units, but declined to essentially no difference by mid-April (Fig. 10). This lessening of differences in diet protein between areas was not statistically significant (test for parallel lines, $P > 0.10$). The lines were not coincident, however ($P < 0.05$), indicating that diet protein was consistently greater in the Valle San Antonio. Biological implications of differences in diet quality will be discussed in a later section.

Diet botanical composition and forage quality interact to determine diet quality. Hence, in Bandelier, where grasses completely dominated the diet, diet quality was highly correlated with grass quality ($r^2 = 0.96$, $P < 0.001$, IVDOM; $r^2 = 0.97$, $P < 0.001$, protein). Browse quality had little effect on diet quality on the burn. Woody plants and grasses were consumed in nearly equal amounts in the Valle San Antonio. Here, diet IVDOM was related to browse IVDOM ($r^2 = 0.50$, $P = 0.058$), but not grass IVDOM. Protein in both grasses and browse was correlated with diet protein ($r^2 = 0.63$, $P = 0.029$, grasses; $r^2 = 0.57$, $P = 0.041$, browse).

Individual samples. Effects of sex, age, location, and time on diet quality were evaluated using fecal samples obtained from elk captured or collected in periods 4-7. Neither sex nor age differences significantly

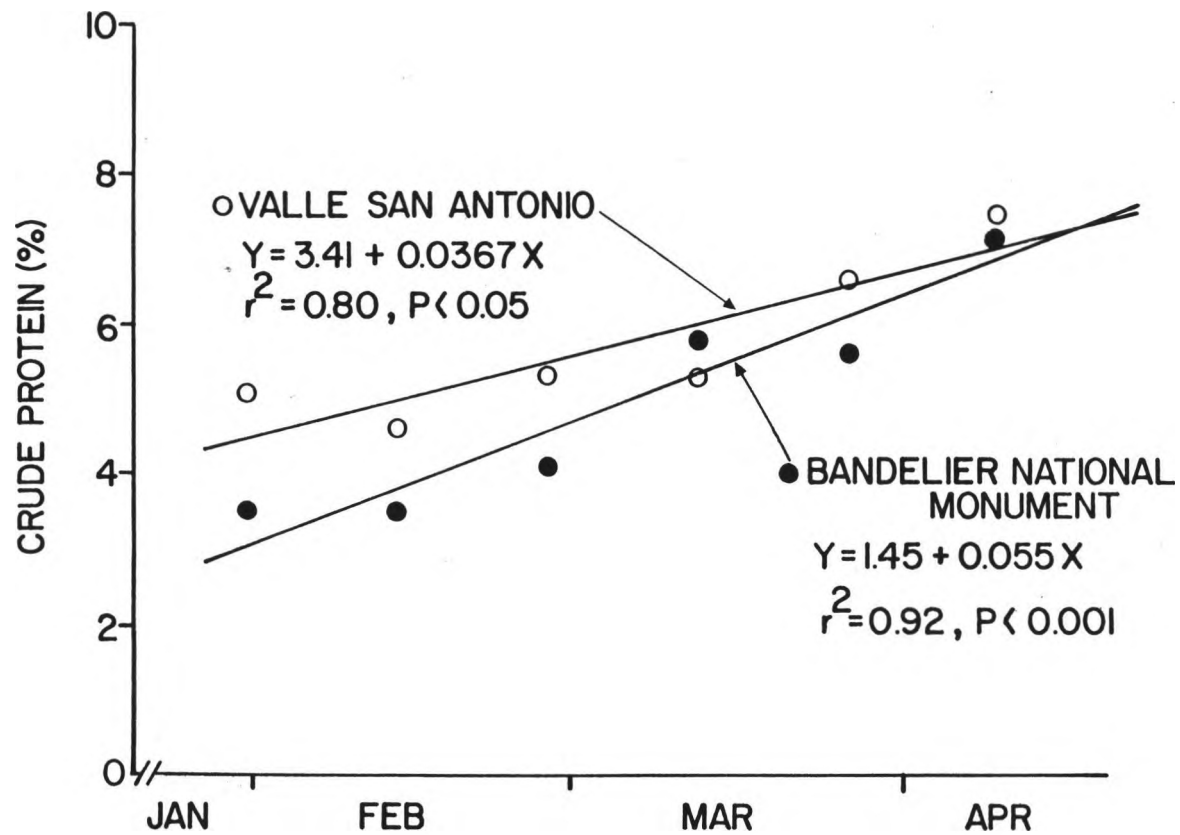


Figure 10. Crude protein, expressed as % organic matter, in diets of elk in the Jemez Mountains, north-central New Mexico, 1980. x = Julian calendar days.

affected diet quality ($P > 0.25$ for all models). Sex and age classes were therefore combined to examine differences among time periods and between locations.

Estimates of diet quality using individual fecal samples were in general similar to those obtained using composite samples. Although diet quality differed between locations, the magnitude of this difference varied among time periods (Table 7, Figs. 11, 12). Elk dietary protein, which increased with advancing season in both areas (Fig. 11), was significantly greater in the Valle San Antonio in periods 5-7 ($P < 0.01$). Differences between areas in diet protein increased with advancing season, unlike results obtained using composite samples. Whether this increase was real or an artifact related to variability inherent in small sample sizes is unknown.

Estimates of diet IVDOM from individual fecal samples were consistently superior in Bandelier ($P < 0.001$, Fig. 12). Temporal increases in diet quality estimates from individual samples paralleled those calculated from composite samples. Marked increases in diet protein occurred by mid-April in both locations (Fig. 11). Although diet IVDOM was not calculated for the final period in the Valle San Antonio, it had increased significantly by early April. In Bandelier, diet digestibility remained constant until mid-April, when a significant increase occurred (Fig. 12).

Summary. Elk diet quality differences were observed among time periods and between study areas. Diet IVDOM and dietary protein increased with advancing season in both locations, although diet IVDOM increased more rapidly in Bandelier than in the Valle San Antonio.

Table 7. Analysis of variance in diet quality of elk captured or collected in the Jemez Mountains, New Mexico, from February-April 1980.

Source	Crude protein (% organic matter)				IVDOM (%) ^a			
	df	MS	F	P	df	MS	F	P
Location	1	6.32	34.19	<0.001	1	391.05	182.43	<0.001
Time	3	9.81	53.12	<0.001	3	114.71	53.51	<0.001
Location x Time	3	0.86	4.66	0.009	2	5.88	2.75	0.081
Residual	29	0.18			28	2.14		

^a*In vitro* digestible organic matter.

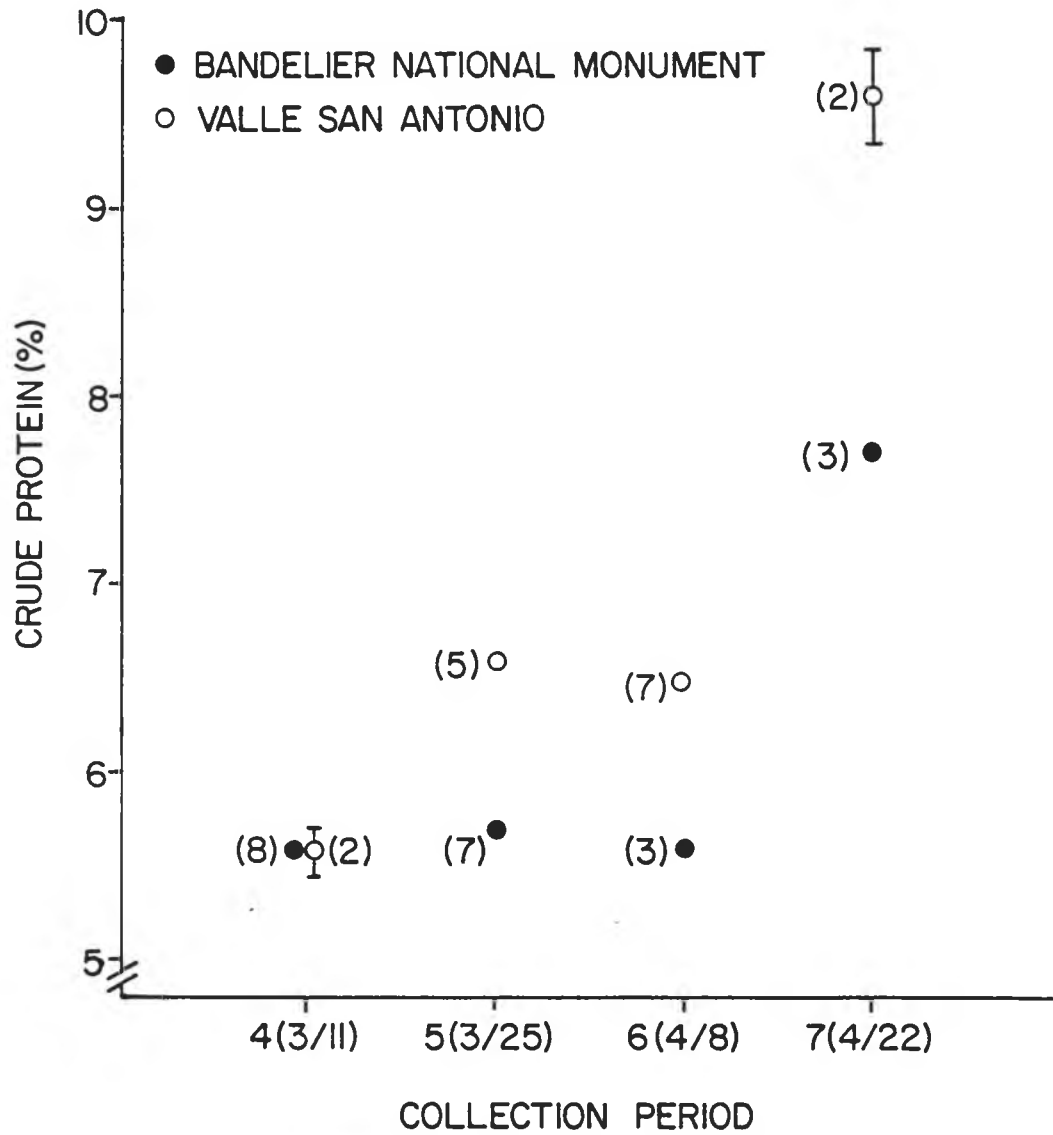


Figure 11. Crude protein ($\bar{x} \pm SE$) in diets of elk captured or collected in the Jemez Mountains, north-central New Mexico, 1980. Dates are mid-points of biweekly sampling periods. Sample sizes are in parentheses. Standard errors < 0.3 are omitted.

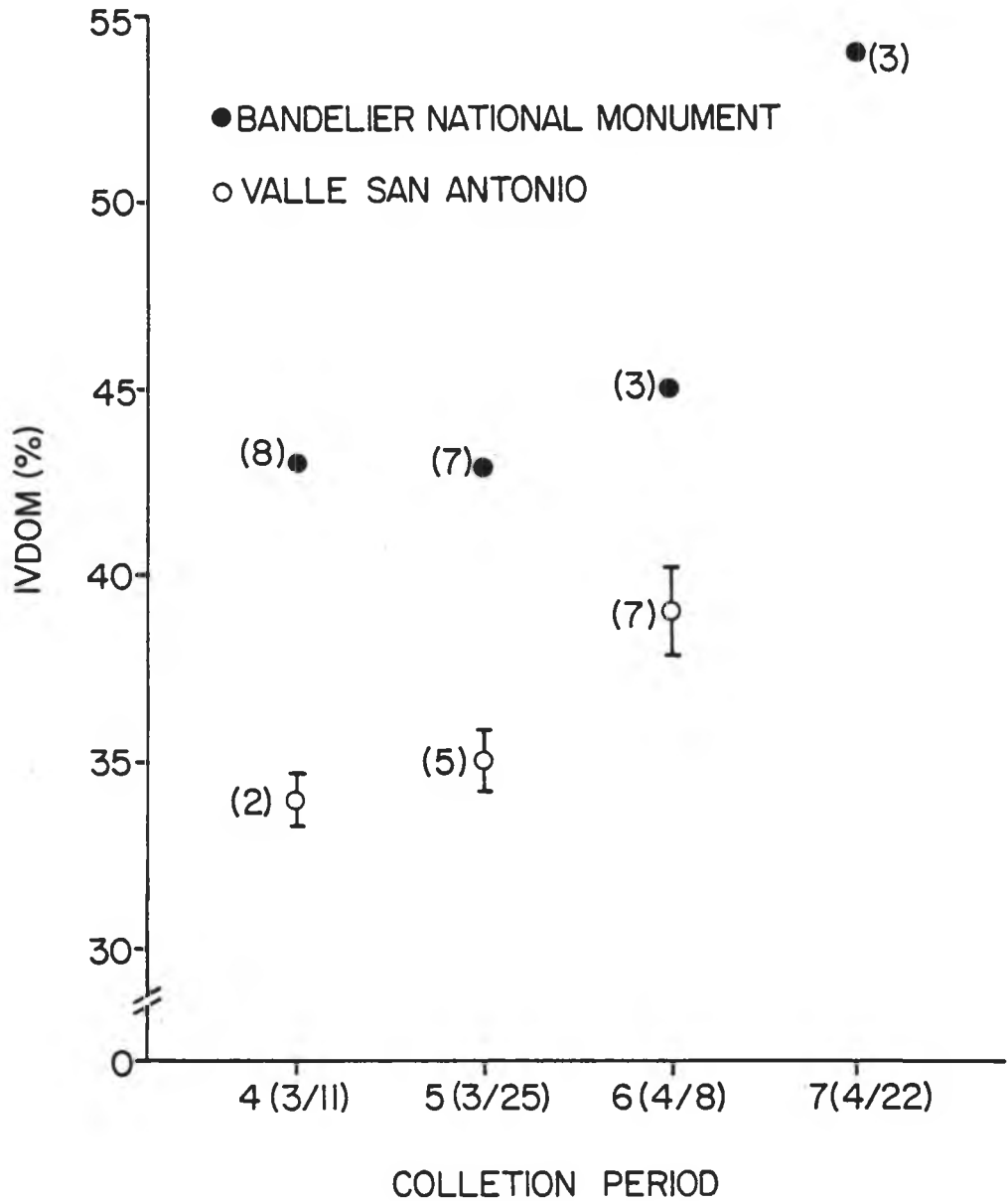


Figure 12. *In vitro* digestible organic matter ($\bar{x} \pm SE$) in diets of elk captured or collected in the Jemez Mountains, north-central New Mexico, 1980. Dates are mid-points of biweekly sampling periods. Sample sizes are in parentheses. Standard errors < 0.3 are omitted.

Diet IVDOM was consistently greater in Bandelier, whereas dietary protein was superior in the Valle San Antonio. Neither sex nor age affected diet quality.

DISCUSSION

Botanical Composition of Elk Diets

Elk diet composition was estimated by microhistological analysis of feces. The validity of using fecal analysis for quantification of herbivore diets has been questioned (Korhage 1974, McReynolds 1977, Pulliam and Nelson 1979, Johnson 1980, Alexander et al. in prep.). Most discrepancies between "known diets" (e.g. bite-count observations, hand-compounded diets, and esophageal and rumen samples) and fecal analysis are related to underestimation of forbs or other highly digestible plant material (Staffon 1976, Pulliam and Nelson 1979, Johnson 1980, Alexander et al. in prep.). The presence of forbs, which averaged less than 10% of the diet in all periods, may have been underestimated in this study. Forbs, however, are typically a minor diet item of Rocky Mountain elk in winter (for review, see Hobbs 1979:25). Few forbs were green in Bandelier until early April, and no evidence of grazing on the green, basal leaves was observed. Growth of forbs had just begun in the Valle San Antonio at the termination of the study. The relatively low digestibilities of most forages analyzed was typical of winter forage quality. Thus, it is unlikely that underestimation of forbs or highly digestible material was important.

The objective of this study was to compare elk diet qualities on 2 winter ranges. Thus, relative, rather than absolute, statements about elk diets were of primary interest. Assuming biases in the fecal analysis technique to be equal between areas, use of this method was justified to meet objectives.

Distribution of elk pellets is not necessarily related to use of habitats for feeding (Collins and Urness 1979). Although it is possible that pellets collected on the La Mesa burn area contained fragments from plants consumed outside the burned area, it is unlikely that elk used other areas to a great extent. Observations of feeding sites, visual sightings of elk feeding, and locations of radio-collared elk (Weber 1981) indicated extensive use of the reseeded burn for feeding. Fewer observations of elk were obtained in the Valle San Antonio than in Bandelier. However, taxa identified in feces from this area were present on south-facing slopes and other feeding sites, where forage samples were collected.

Valid comparison of results from composite vs. individual samples was infeasible, due to disparities in sample sizes and collection dates. However, because feces from trapped elk can be accurately dated, and sex and age classes assigned, these samples provide information unobtainable from samples collected from random pellet groups. In addition, these samples allow calculation of variance in diets among individuals. Many more samples, however, can be collected randomly in the field, perhaps better representing diets of the herd using the range.

Diets estimated from individual samples were less diverse than those from composite samples (Table 4). Presumably this difference was related to the number of pellet groups sampled, as well as the number of fields examined per sample. Composite samples represented an average of 26 pellet groups, while a maximum of 8 elk were handled within a single period in either location, and in 3 instances only 2 were sampled. It is highly likely that several pellet groups from a single elk were sampled for inclusion in a single composite sample, especially around

trap sites. However, the number of elk represented in composite samples probably exceeded that of elk trapped or collected, despite this potential duplication in composite samples.

Elk diets in the Jemez Mountains were typical of Rocky Mountain elk; grasses usually dominate their winter diets (Kufeld 1973, Leege et al. 1977). The paucity of forbs was also typical of elk winter diets (Kufeld 1973, Hobbs et al. 1981); other studies of elk in New Mexico revealed similar results (Lang 1958, Gates 1967, Findley et al. 1975). As discussed previously, forbs did not begin new growth until early April in Bandelier and were withered and often shattered prior to this time. Although inflorescences had been grazed from many of the composites, it is unknown when this occurred. Hobbs (1979) suggested that the dispersion of forbs in space, their small size, and the presence of a dense grass canopy contributed to the relative unimportance of forbs in elk winter diets in Colorado. I believe similar reasons accounted for the minor quantities of forbs in the diets of the Jemez Mountain elk.

Composition of elk diets in the 2 areas was markedly different. Grasses formed the bulk of elk diets in Bandelier, but were consumed nearly equally with browse in the Valle San Antonio. Whether grasses or browse dominate winter diets of elk is largely related to relative availability of these forage classes (Kufeld 1973, Leege et al. 1977). Because forage availability was not quantitatively assessed during this study, a direct comparison between Bandelier and the Valle San Antonio of the availability of grasses and browse was not possible. It is probable, however, that grasses were more available to elk on the burn due to the scant snow cover there and the reseeding following the La Mesa fire.

Although snow depths were not systematically recorded, most of Bandelier, with the exception of heavily shaded areas and north-facing slopes, was snow-free by late February. Subsequent snowfall disappeared within a day or 2, due to warm temperatures and lack of shade on the burn. In contrast, snow depths in the Valle San Antonio exceeded 1 m in the valley floors until late March. South-facing slopes were generally snow-free within days after a storm, but all other areas remained covered until early April when snowmelt began. Precipitation during the study totaled 152 mm, primarily as snow, at the Fenton Hill weather station in the Valles Caldera. Bandelier recorded only 79 mm of precipitation (primarily snow) during this time. The mean daily maximum temperature in Bandelier was 12.3 C, contrasting with 5.0 C in the Valle San Antonio.

In most snow-covered areas in the Valle San Antonio, only culms of the tallest grasses, e.g. Thurber fescue, were available above the snow. Evidence of elk pawing through snow to obtain herbaceous forage was never observed on the burn, but was common in the Valle San Antonio.

Reseeding of the La Mesa burn produced an abundance of grasses, especially sheep fescue and slender wheatgrass. These 2 species formed 80% of the diet in Bandelier and dominated the flora in severely burned sites (Appendix B).

Increases in herbaceous material are common in post-fire habitats (Weaver 1967, Biswell 1972, Foxx and Potter 1978), and availability of herbs may increase due to the reduction in standing litter (Daubenmire 1968). Thus, the combined effects of the La Mesa fire and differences in snow depths, by affecting forage availability, probably accounted for major differences between diet compositions in the 2 areas. Hobbs

et al. (1981), however, found a lack of correspondence in diet composition and prewinter (fall) biomass of grasses, forbs, and shrubs in some habitats. Elk selected browse to supplement low protein in grasses.

Although availability affects diet selection, forage quality may also influence diet choices. No clear relationship was evident between ranks of species in the diet and forage quality. For example, IVDOM and protein in sheep fescue were below the mean values for grasses, although this species constituted 70% of the diet on the burn. Protein in Arizona fescue, the main forage in the Valle San Antonio, averaged 1.4 units less than the mean for graminoids in this area, although IVDOM was not below average. Relationships between consumption and forage quality were more evident when comparing forage classes. In Bandelier, where grasses constituted over 90% of the diet, grasses were significantly more digestible than was browse. However, differences in quality between grasses and browse were less pronounced in the Valle San Antonio, where browse and grass were consumed in nearly equal proportions.

Phenological development may have influenced diet selection. In Bandelier, where grasses dominated, basal leaves of most grasses were green by late February. This condition did not exist in the Valle San Antonio until late March, and included only south-facing slopes. Sheep fescue, which accounted for 70% of the diet in Bandelier, was the only herbaceous species to remain green throughout the winter on the burn; nearly every plant appeared to have been grazed. Fescues were also important in the diet in the Valle San Antonio. Some basal leaves of Arizona fescue were green in mid-January, but most plants were dormant by late February. Sedges, another important forage in the Valle San

Antonio, were located in geothermal sites along meadow creeks, where they remained green throughout the winter.

Temporal changes in diet composition were minimal in both areas (Fig. 4). In the Valle San Antonio, observed increases in grass consumption in early April may have been due to increased quality and availability of grasses. Prior to this time, consumption of more grass may have been limited by energetic costs of feeding on a forage not readily available. In Bandelier, grasses averaged 90% of the diet, and, unlike browse, quality of grasses increased steadily during the study. Assuming availability of grasses remained constant or increased as spring approached, a shift in diet botanical composition on the burn would not be expected at this time.

Forage Quality

Grasses and browse analyzed in this study exhibited typical disparities in quality. Grasses were uniformly more digestible than browse, as reported in other studies (Cook 1972, Palleson 1979, Hobbs et al. 1981). Grasses contain more cell wall than do other forages but possess little lignin, a relatively indigestible fiber component (Van Soest 1975). *In vitro* digestibilities ranged from a low of 17% in shrubby cinquefoil to a high of 72% in prairie junegrass. Variability in IVDOM among species was considerable (Table 5), and IVDOM of many browse samples from the Valle San Antonio equalled IVDOM of grasses collected during the same period.

Differences in protein between forage classes were not significant in the analysis of variance. Browse typically contains more protein than does grass (Hickman 1975, Blair et al. 1977, Hobbs et al. 1981).

In this study, grass protein, although less than that in browse initially, increased with advancing season and surpassed that in browse by April. Increases in quality of grasses with initiation of spring growth are widely reported (Cook and Harris 1950, Burzlaff 1971, Hickman 1975, Pulliam and Nelson 1979) and relate to translocation of nutrients to new, growing tissues (Beaty and Engel 1980, Hobbs 1979). The change in quality with advancing season is primarily due to changes in proportions of dead vs. live material within the plant (Beaty and Engel 1980). For instance, nitrogen content of dead leaves may be constant year-round, but the proportion of dead leaves in the plant is not. In contrast to grasses, browse forages showed no measurable changes in quality with advancing season. This lack of variability in winter browse quality has been previously noted (Dietz et al. 1958, Dietz 1967, Hickman 1975, Blair et al. 1977, Hobbs et al. 1981).

Mean quality of browse from the Valle San Antonio was superior to that of Bandelier browse (Table 5), although these differences were not significant. This disparity may have been related to the proportion of conifers vs. deciduous species sampled in the 2 areas. Eleven of 20 samples in the Valle San Antonio were of evergreens, contrasting with only 2 of 8 from the burn. Evergreens have been shown to contain more protein and less fiber in winter than do deciduous shrubs (Lay 1957, Dietz 1967).

Oelberg (1956) enumerated several factors affecting nutritive quality of forage, including stage of maturity, soils, climate, plant species, and range condition. By affecting weather patterns, elevational differences between the study areas produced differences in phenological development of plants. Soils in the areas are dissimilar (J. Nyhan,

pers. commun.), as is plant species composition. Despite these differences between sites, the quality of elk forages was similar. This similarity can perhaps be explained by the ability of elk to feed selectively, as demonstrated by Hobbs et al. (1981). Only forages consumed by elk were analyzed; these were not necessarily representative of total forage resources available. Although species composition of the 2 winter ranges was not identical, elk presumably selected the most nutritious forages available, within energetic constraints.

Comparison of species common to both areas also revealed no difference in IVDOM or protein. Fire-effected increases in forage quality may quickly disappear (Ahlgren and Ahlgren 1960, Dills 1970). Lloyd (1971) reported that increases in plant protein in response to burning were essentially absent by 24 months; his studies included sheep fescue. Our study commenced 30 months after the La Mesa fire, and changes in forage quality in response to fire, if they did indeed occur, may well have disappeared.

Diet Quality

Any attempt to estimate diet quality in wild ungulates is subject to numerous problems. Diet botanical composition may not be correctly approximated; biases associated with the fecal analysis technique used in this study were discussed previously. In addition, the validity of relating *in vitro* digestion of single species samples to *in vivo* digestibility of mixed species diets has been questioned; *in vivo* and *in vitro* associative effects, positive or negative, may occur (Milchunas et al. 1978, Mould 1980). The weighted mean method used in this study (i.e. multiplying IVDOM x diet % for each species and adding these products),

however, provided better predictions of *in vivo* digestibilities of mule deer diets than did *in vitro* digestion of species mixtures (Milchunas et al. 1978).

Numerous studies cite the superior quality of diets selected by grazing domestic ruminants vs. hand-clipped forage samples (Weir and Torell 1959, Cable and Shumway 1966, Bredon et al. 1967, Rao et al. 1973). In these studies, no attempt was made to simulate diet composition, either by plant species or parts; rather, entire plots were clipped or mowed. Plant parts within a species may differ significantly in nutritional value (Cook and Harris 1950, Cable and Shumway 1966, Cowan et al. 1970).

In our study, forage samples were collected by simulating removal of plant parts from previously grazed or browsed plants. For example, culms of stemmy grasses such as slender wheatgrass or bottlebrush squirreltail were included in only small amounts. Elk generally pushed these culms aside to consume basal leaves. Nonetheless, the overall quality of forage samples was probably less than that of forages actually consumed by elk, because direct feeding observations were not made. Hence, diet quality was probably underestimated. Schwartz et al. (1977) also believed they underestimated pronghorn (*Antilocapra americana*) diet quality by clipping less nutritious plant parts than those selected by pronghorn.

Not all taxa identified in fecal analysis were collected during the appropriate sampling period. Species percentages were therefore normalized to sum to 100. The proportions of the diets analyzed for nutritional value ranged from 68-84% in the Valle San Antonio and from 82-96% in Bandelier. It is possible that elk forages not analyzed were higher

in quality than those sampled. Conversely, diet quality could have been overestimated by normalization, which would inflate importance of major forage species.

Forage quality was more variable than diet quality, indicating the ability of elk to maintain relatively constant diet quality when confronted with variably inadequate resources. During January and February, when forage quality was at a minimum, elk diets were superior in protein and digestibility to the mean values for grasses and browse. The single exception was that browse protein in the Valle San Antonio exceeded that in the diet. Rapid increases in quality of grasses in late February and early March were not equalled by diet quality increases; however, diet quality generally improved steadily from January-April. McReynolds (1977) and Hobbs (1979) also noted that elk diet quality generally fluctuated less than the average quality of forages on offer.

No differences in diet quality were found among sex and age classes of elk, although sample sizes may have been too small to detect real differences. Little information has been published regarding diet differences related to sex and age in wild ruminants. Red deer hinds have been reported to occupy separate wintering areas with superior forage quality relative to ranges occupied by stags (Watson and Staines 1978). Bergerud (1972) reported differences in diets selected by different age classes of caribou (*Rangifer tarandrus*). Sinclair (1974), however, found no difference in diet quality among sex and age classes of African buffalo (*Syncerus caffer*). Bighorn sheep (*Ovis canadensis*) classes also did not differ in forage preference (Johnson 1980).

Neither grasses nor browse differed in quality between Bandelier and the Valle San Antonio. Disparities in diet quality between the areas

were therefore caused by differences in diet composition and the differing qualities of grasses and browse. The prevalence of grasses in elk diets from Bandelier resulted in superior diet IVDOM at this site in 2 ways. First, grasses were uniformly more digestible than was browse. Grasses were never more than 60% of the diet in the Valle San Antonio, but composed up to 98% of the diet in Bandelier. Second, IVDOM of grasses increased rapidly in spring, whereas browse IVDOM remained relatively constant, thereby widening the disparity in diet IVDOM between areas.

The comparatively slight differences in dietary protein between areas seemed anomalous because protein in browse was in general not significantly greater than protein in grasses. In late January, however, protein in Valle San Antonio browse was over 4 units greater than protein in Bandelier grasses. This difference diminished with time, as grasses increased in quality while quality of browse remained constant. Thus, dietary protein in the areas was essentially equal by April.

One might have expected dietary protein in Bandelier to exceed that in the Valle San Antonio at an earlier date, due to the rapid increase in quality of grasses at the lower elevation. Sheep fescue, however, constituted 70% of the diet in Bandelier, yet contained less protein than any of the grasses sampled in this area and did not increase in protein proportionally with other grasses. Thus, overall increases in quality of grasses in Bandelier were insufficient to elevate diet protein above that in the Valle San Antonio.

The availability of dietary protein to the ruminant, however, was probably less in the Valle San Antonio, due to the presence of tannins in woody plants (Swain 1979). Browse constituted nearly 50% of the

dietary protein in the Valle San Antonio. Tannins, by complexing with soluble plant proteins, inhibit the nutritional availability of these proteins. Tannins also disrupt the activity of digestive enzymes and rumen microbes, further reducing the digestibility of foods in the rumen (Swain 1979). In addition, urea recycling increases as dietary protein decreases, thereby partially compensating for dietary nitrogen deficiencies (Hume et al. 1970, Mould 1980). Hence, differences in diet protein may not have been as large *in vivo* as they seemed from forage quality analyses alone.

Estimated diet quality, particularly dietary protein, was marginal, but probably adequate for maintenance of elk in winter. Dietary protein averaged 5%. Mould and Robbins (1981) estimated that diets containing less than 5% protein would not meet maintenance requirements of elk for nitrogen. Diet quality estimates for elk in our study were comparable to results reported by Hobbs et al. (1981) for tame elk in Rocky Mountain National Park, Colorado. During November-March, dietary protein of these animals ranged from 4.6-6.3%. In the Colockum elk herd in central Washington, dietary protein ranged from 3.6-21.4% in 1973 (Schommer 1978) and from 7.6-14.0% in 1974-1975 (McReynolds 1977) during the same period. Elk maintained relatively high dietary protein in winter by feeding in cultivated wheat fields (*Triticum* spp.).

Diet digestibility estimates in our study were remarkably similar to results from the Colorado study (Hobbs et al. 1981). Diet IVDOM of elk in the Jemez Mountains ranged from 33-46% and in Colorado from 35-47% (Hobbs et al. 1981). Again, values from Washington were relatively high, ranging from 46-68% (Schommer 1978). Ward (1971) reported an average digestibility of 48% for grasses consumed by elk wintering in Wyoming.

In general, quality of elk diets in our study was comparable to that of other Rocky Mountain elk.

How can these diets be explained in terms of optimal foraging strategy and diet selection theory? If, as suggested by Ellis et al. (1976), herbivores optimize nutritional balance in feeding, then we can assume that elk in the Jemez Mountains consumed foods to best meet simultaneous demands for nitrogen and energy. The primary components of diet selection include consumer food requirements, selectivity, preference, and food availability (Ellis et al. 1976). Presumably, food requirements of elk were similar in the 2 areas, although differences in temperature and snow depths may have resulted in higher activity and maintenance costs in the Valle San Antonio. Differences in diet selectivity, which relate to reproductive state, animal size, and degree of satiation, were also assumed to be minimal. Potential differences between areas in preference relate to forage quality and availability. When food is less available, preference becomes relatively less important in the diet selection process (Ellis et al. 1976). Availability in turn is affected by food density and snow cover. Thus, 3 factors may have contributed to observed differences in diets selected: food quality, food density, and snow characteristics. Forage quality did not differ between locations, but did differ between forage classes. The suspected differences in availability of herbaceous forage, as effected by reseeding and snow depth, were discussed previously. In light of the preceding assumptions, the following explanation of diet selection in the 2 areas is proposed.

If protein in grasses on the burn was adequate for maintenance of elk condition, then Bandelier elk would benefit by not selecting browse

because: 1) browse was probably less abundant and more patchily distributed than grass (Appendix B) and thus required more energy to obtain; and 2) browse was less digestible than grass and therefore an inferior source of energy.

In the Valle San Antonio, consumption of browse provided adequate dietary protein, although diet IVDOM was concomitantly lowered. Elk in the Valle San Antonio may have consumed as much grass as possible within energetic constraints of finding and acquiring this food. Grasses were equal or superior to browse in quality. Thus, availability, not quality, of herbaceous forage probably limited its intake in the Valle San Antonio. Diet selection was therefore largely a function of forage availability, but was also influenced by differences in qualities of grasses vs. browse.

Unlike our results, Hobbs (1979) found elk diet quality unrelated to forage availability. That is, diet quality was relatively constant among habitats that differed widely in biomass of grasses, forbs, and shrubs. However, only biomass differed among habitats studied; abiotic influences were presumably similar. Schwartz et al. (1977) also found no differences in pronghorn diet quality between pastures lightly and heavily grazed by cattle.

Hobbs (1979) concluded that elk were generalists, capable of altering diet botanical mix to meet nutritional requirements. He proposed that elk selected browse to supplement relatively low protein in grasses, at the expense of decreased diet digestibility. Field (1976) reported a similar inclusion of browse in the diet by African buffalo as a "protein supplement" when protein in grasses declined. In Colorado, elk diet quality was similar among habitat types because botanical composition

of diets was similar (Hobbs 1979). In the Jemez Mountains, diet qualities of elk were dissimilar due to differences in diet botanical composition.

What are the consequences of these differences in diet quality on nutritional status of elk? Hobbs et al. (1981) believed that protein deficiencies were more costly than energy deficits for elk in winter, thereby explaining the consumption of browse by elk at the expense of lowered diet digestibility. Nitrogen intake is especially important during advanced pregnancy, due to the negative nitrogen balance typically incurred by lactating females (Maynard and Loosli 1969). Energy contained in forage structural components would be unavailable without a supply of nitrogen adequate for microbial growth (Cowan et al. 1970), because growth of fiber-digesting bacteria is most commonly limited by a scarcity of nitrogen (Schwartz and Gilchrist 1975). Birth weights of domestic lambs (Christenson and Prior 1976) and white-tailed deer fawns (*Odocoileus virginianus*) (Kirkpatrick et al. 1975) were significantly affected by dietary protein and an increase in dietary protein in captive mule deer produced heavier deer and larger antlers (Robinette et al. 1973). Increases in body size (Einarson 1946, Taber 1956) and densities (Taber 1956) of black-tailed deer (*O. hemionus columbianus*) occurred on ranges providing browse higher in protein than that in surrounding areas. Thus, higher levels of dietary protein in the Valle San Antonio may have resulted in better condition of animals wintering there. However, differences in dietary protein between locations may not have been as large *in vivo*, as discussed previously.

Assuming that dietary protein was adequate, though marginal, for elk wintering in the Jemez Mountains, how important were observed differences

in diet IVDOM? Digestible energy, which is highly correlated with digestible dry matter (Robbins et al. 1975, Milchunas et al. 1978, Schommer 1978), may be the most commonly deficient nutrient for ruminants (Maynard and Loosli 1969, Dietz 1970, Halls 1970). Dietary energy was related to lamb vigor at birth and daily weight gain in ewes (Christenson and Prior 1976) and weight gain, skeletal and organ size, and fat deposits in white-tailed deer fawns in autumn (Verme and Ozoga 1980). Diets high in protein but low in energy may be metabolically disruptive, due to insufficient retention and utilization of nitrogen (Mould 1980, Verme and Ozoga 1980). Ammann et al. (1973) concluded that ruminant diets containing less than 50% digestible energy were probably inadequate for maintenance. Diets of elk did not exceed 50% IVDOM in either of our study areas. Differences in diet digestibilities are particularly important when energy intake approaches critical, i.e. sub-maintenance, levels. Blaxter et al. (1961) reported a 100% increase in weight gain in domestic sheep when diet digestibility was increased from 50 to 55%. Hence, the mean difference of 5 units in diets of elk in Bandelier vs. the Valle San Antonio may have produced large differences in animal condition during the critical late winter-early spring period.

Protein and energy are both necessary for the well-being of ruminants. The complex inter-relationship of these nutrients precludes a simple answer to the question of which nutrient is more important to the animal's welfare. Use of the simulation model to predict elk nutritional status allowed integration of effects of dietary protein and energy. The model is not constrained by empirical data from feeding trials; rather it operates at a physiological level (e.g. predicting

rumen microbial fermentation rates) to predict changes in energy and nitrogen balance effected by different dietary regimes.

Simulation of elk condition from January to April predicted steady declines in weight throughout the winter, both in burned and unburned areas (Fig. 13). However, proportions of body weight as fat were dissimilar between areas during February-April, and marked differences were predicted in energy and nitrogen balance.

Losses in total weight in yearling elk from Bandelier paralleled those in Valle San Antonio elk through most of the winter. Predicted weight losses were 10% in Bandelier and 13% in the Valle San Antonio. However, simulated elk in Bandelier began to gain weight by early April and continued to do so through April. In contrast, no weight gain was predicted for animals in the Valle San Antonio, and a sharp decline in total weight occurred in late April. Changes in total body weight are best understood in terms of the 2 components of this weight, viz. lean body and fat.

Deficits in dietary protein in Bandelier resulted in a 4% loss of lean body by mid-March (Fig. 13), at which time diet protein equalled simulated requirements for protein. Lean body subsequently increased 5% and a positive nitrogen balance of 18 g/day was predicted by late April. Initial nitrogen deficits in the Valle San Antonio diet were slight, thus no substantial losses in lean body occurred (Fig. 13). A positive nitrogen balance was achieved by late February, 10 days earlier than in simulated Bandelier elk; lean body weight subsequently increased until late April. The total depletion of fat stores at this time resulted in substantial catabolism of lean body to meet maintenance energy requirements. This process created a nitrogen deficit of

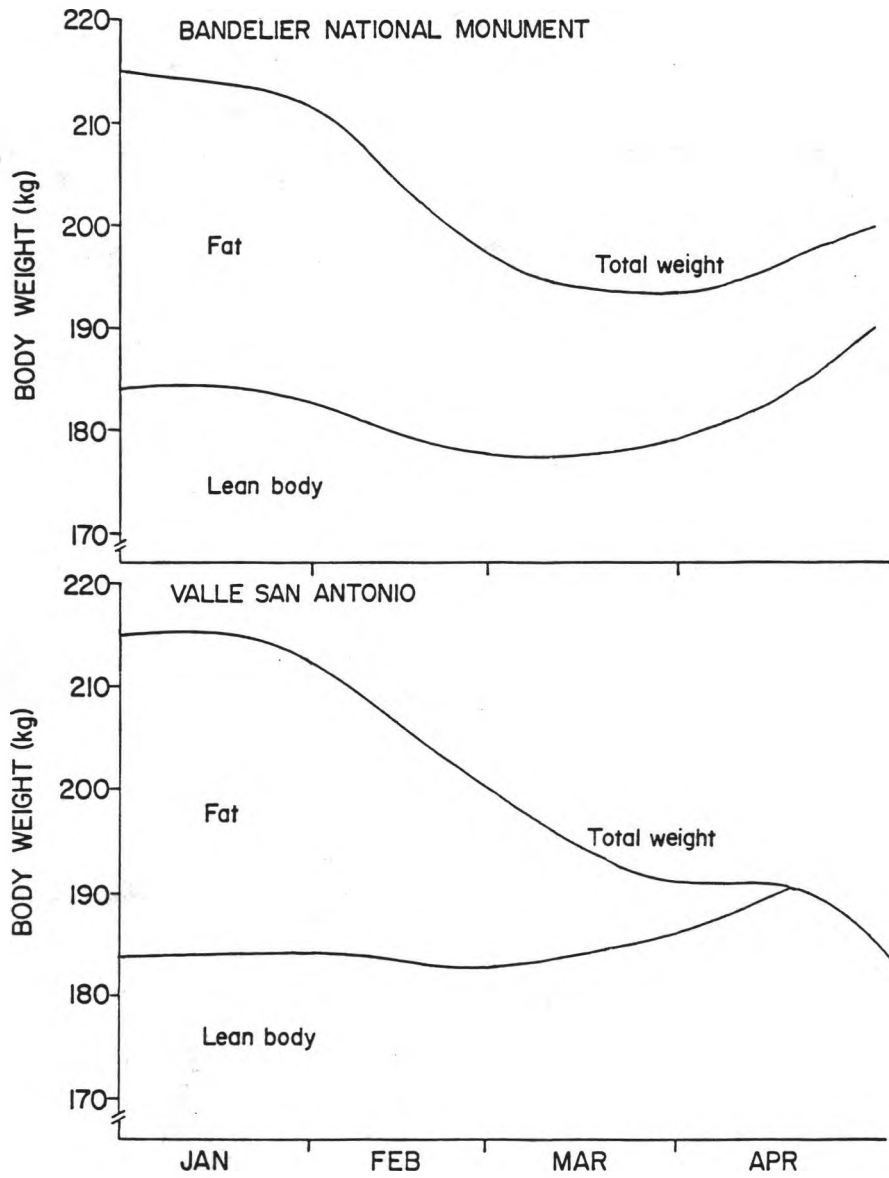


Figure 13. Simulation of changes in body weight of a yearling elk in the Jemez Mountains, New Mexico, 1980.

70 g/day. Until this time, nitrogen balance had been quite similar between locations, paralleling observed similarities in dietary protein.

Although slight increases in lean body were predicted in both areas by early March, fluctuations were minimal. Hence, losses in total body weight were effected primarily by depletion of fat. Energy intake was insufficient to meet energy requirements until early April in Bandelier. Consequently, fat declined from an initial high of 14% body weight to a low of 6%. A slight increase in fat was predicted by the end of April, when energy surplus was 1170 kcal/day. Predicted fat stores in elk from the Valle San Antonio were lower at all times than those in Bandelier elk. Energy deficits fluctuated in the Valle San Antonio, but were never overcome. Fat depletion occurred more rapidly in this area, and total exhaustion of fat was predicted by mid-April. At this time, a sharp increase in the energy deficit occurred as a result of the relatively less efficient conversion of lean body (vs. fat) to energy. Although recent studies indicate complete exhaustion of fat prior to lean body catabolism is unlikely to occur in a wild ruminant (Carpenter and Torbit 1980), the greater predicted loss of fat in the Valle San Antonio was indicative of inferior digestible energy resources in this area.

In summary, because energy and protein intake in Bandelier elk exceeded maintenance levels by early April, an increase in total weight was possible at this time. However, adequate diet protein was insufficient to overcome large deficits in energy in the Valle San Antonio elk. Body weight continued to decline, and the rate of decline accelerated sharply when fat was depleted. Thus the critical difference in diet quality between areas was in diet IVDOM, not in dietary protein.

Although the model is constructed from the best available sources on ruminant physiology, discrepancies between the model predictions and empirical data exist. For example, complete depletion of fat stores prior to lean body catabolism has been proven incorrect (Carpenter and Torbit 1980) and the model overpredicts weight loss of animals on low quality diets by failing to account for compensatory behavioral and metabolic responses of animals near starvation (D. Swift, pers. commun.). An additional problem is the lack of meteorological data input other than temperature. Snow depths in the Valle San Antonio far exceeded those in Bandelier. Thus additional energy expended in locomotion and forage acquisition in the Valle San Antonio may have further widened the observed disparity in energy balance between the 2 areas. Nonetheless, biases in the model generally operated equally on simulated elk from the 2 locations, justifying comparison of model predictions.

Only if model predictions can be tested empirically are they of value. Trapping of elk in the Jemez Mountains provided such testing. Results of trapping corroborated model predictions--elk in the Valle San Antonio weighed significantly less than elk in Bandelier (Weber 1981). Differences in condition of elk were assumed to be attributable to differences in winter range qualities (Weber 1981).

SUMMARY

Winter diets of elk were compared between a recently burned, montane winter range (Bandelier National Monument) and an unburned, upper montane range (Valle San Antonio) in the Jemez Mountains of New Mexico. Dietary IVDOM was significantly greater in Bandelier, whereas dietary protein was superior in the Valle San Antonio. Differences in dietary protein, however, may have been less substantial *in vivo*, due to the presence of tannins in diets of elk in the Valle San Antonio and probable greater urea recycling in elk from Bandelier.

Disparities in diet quality between areas were a function of differences in diet botanical compositions and in qualities of grasses and browse. Grasses, which dominated diets of elk in Bandelier, were more digestible than was browse. Temporal changes in quality were also more rapid in grasses, further widening differences in diet IVDOM. Browse protein exceeded that in grasses during most of the study, resulting in higher dietary protein levels in the Valle San Antonio.

Reseeding of grasses and the scant snow cover on the burn probably resulted in greater availability of herbaceous plants in this area. Thus, differences in forage availability, rather than in forage quality, were believed responsible for differences in diet botanical compositions between study areas. Forage quality was more variable than was diet quality, indicating the ability of elk to maintain relatively constant diet quality despite large fluctuations in forage quality.

Potential effects of differences in diet quality on nutritional status of elk are difficult to predict, because effects of protein and energy are inextricably related in the ruminant. Simulation modeling,

however, predicted greater weight losses in elk from the Valle San Antonio, due to the larger energy deficit incurred there. Superior dietary protein was ineffective in preventing these losses.

Although diet quality of elk on the burn exceeded that of elk in the Valle San Antonio, this phenomenon could not be attributed to fire alone; variables other than burning were not controlled. Elevational differences, resulting in dissimilarities in snowfall and plant communities, may have been largely responsible for observed differences in diet qualities.

Fire is an important source of perturbation in the Jemez Mountains, and preferential use of burned areas by elk has long been recognized. However, whether increased use of burns is a function of improved forage quality and quantity or merely alteration of habitat structure remains unknown. Effects of fire on elk diets and, ultimately, animal condition, would best be studied experimentally by selection of paired plots, followed by controlled burning. Forage responses and elk diets and condition could be measured at periodic intervals. Use of tame elk would allow control of location and date of grazing and, most importantly, replication of diets.

This study reports the first estimates of winter diet quality of wild elk in the Rocky Mountains. Further investigations will hopefully enhance our understanding of winter range qualities and their association with elk nutritional status and, ultimately, population performance.

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Appendix A. Plants submitted as voucher specimens for microhistological analysis of elk fecal material and other common plants in the Jemez Mountains, north-central New Mexico.

Botanical name ^a	Common name	Location	
		BNM ^b	VSA
Graminoids ^c			
<i>Agropyron desertorum</i>	crested wheatgrass	x	
<i>A. smithii</i> * ^d	bluestem wheatgrass	x	x
<i>A. subsecundum</i>	bearded wheatgrass		x
<i>A. trachycaulum</i>	slender wheatgrass	x	x
<i>Agrostis</i> spp.	bentgrass	x	x
<i>Andropogon gerardii</i>	big bluestem	x	
<i>A. scoparius</i>	little bluestem	x	x
<i>Aristida arizonica</i>	Arizona threeawn	x	
<i>A. longiseta</i>	red threeawn	x	
<i>Blepharoneuron tricholepis</i>	pine dropseed	x	x
<i>Bouteloua curtipendula</i> *	sideoats grama	x	
<i>B. gracilis</i>	blue grama	x	x
<i>Bromus ciliatus</i>	fringed brome	x	
<i>Carex</i> spp.	sedge	x	x
<i>Dactylis glomerata</i>	orchardgrass	x	x
<i>Danthonia parryi</i>	Parry danthonia		x
<i>Deschampsia caespitosa</i>	tufted hairgrass		x
<i>Elymus canadensis</i>	Canada wildrye		x
<i>Festuca arizonica</i>	Arizona fescue		x
<i>F. elatior</i>	meadow fescue	x	
<i>F. octoflora</i>	sixweeks fescue	x	

Appendix A. (continued).

Botanical name	Common name	Location	
		BNM	VSA
<i>F. ovina</i>	sheep fescue	x	
<i>F. thurberi</i>	Thurber fescue		x
<i>Festuca</i> spp.	fescue	x	
<i>Hordeum jubatum</i>	foxtail barley	x	
<i>Juncus</i> spp.	rush	x	x
<i>Koeleria cristata</i>	prairie junegrass	x	x
<i>Muhlenbergia montana</i>	mountain muhly	x	x
<i>M. wrightii</i>	spike muhly	x	
<i>Phleum pratense</i>	timothy		x
<i>Poa fendleriana</i>	mutton bluegrass	x	
<i>P. pratensis</i>	Kentucky bluegrass	x	x
<i>Sitanion hystrix</i>	bottlebrush squirreltail	x	x
<i>Sporobolus cryptandrus</i> *	sand dropseed	x	
<i>Stipa</i> spp.*	needlegrass		x
Forbs			
<i>Achillea lanulosa</i>	western yarrow		x
<i>Allium cernuum</i> *	nodding onion	x	
<i>Antennaria parvifolia</i>	pussytoes	x	
<i>Artemisia carruthii</i> *	Carruth sagebrush	x	x
<i>A. dracunculoides</i> *	false tarragon	x	
<i>A. frigida</i> *	fringed sagebrush	x	x
<i>A. ludoviciana</i>	Louisiana sagebrush	x	
<i>Aster</i> spp.	aster	x	x
<i>Bahia dissecta</i> *	ragleaf bahia	x	

Appendix A. (continued).

Botanical name	Common name	Location	
		BNM	VSA
<i>Castilleja integra</i>	wholeleaf paintedcup	x	
<i>Chenopodium</i> spp.	goosefoot	x	
<i>Chrysopsis villosa</i>	hairy goldaster	x	x
<i>Cirsium</i> spp.	thistle	x	
<i>Cryptantha jamesii</i> *	James cryptantha	x	
<i>Descurainia pinnata</i> *	pinnate tansymustard	x	
<i>Equisetum laevigatum</i> *	smooth horsetail	x	x
<i>Erigeron</i> spp.	fleabane		x
<i>Eriogonum jamesii</i>	James eriogonum	x	
<i>E. racemosum</i>	redroot eriogonum	x	
<i>Eupatorium</i> spp.	eupatorium	x	
<i>Fragaria bracteata</i>	bracted strawberry		x
<i>Geranium caespitosum</i>	geranium	x	
<i>Hymenoxys richardsonii</i>	pingue	x	
<i>Lappula redowskii</i> *	stickseed	x	
<i>Lithospermum multiflorum</i> *	manyflower gromwell	x	
<i>Lotus wrightii</i> *	Wright deervetch	x	
<i>Penstemon</i> spp.	penstemon	x	
<i>Petalostemon</i> spp.	prairieclover	x	
<i>Plantago patagonica</i>	Patagonia Indianwheat	x	
<i>Polygonum</i> spp.	knotweed	x	
<i>Potentilla hippiana</i>	horse cinquefoil	x	
<i>P. pulcherrima</i>	beauty cinquefoil	x	
<i>Senecio</i> spp.	groundsel	x	x
<i>Sisymbrium linifolium</i> *	garlicmustard	x	

Appendix A. (continued).

Botanical name	Common name	Location	
		BNM	VSA
<i>Thelesperma</i> spp.	greenthread	x	
<i>Thermopsis pinetorum</i>	pine thermopsis	x	
<i>Thlaspi</i> spp.	pennycress	x	
<i>Townsendia exscapa</i>	stemless townsendia	x	
<i>Verbascum thapsus</i> *	flannel mullein	x	
Trees and shrubs			
<i>Abies concolor</i>	white fir	x	x
<i>A. lasiocarpa</i> *	subalpine fir		x
<i>Acer glabrum</i>	Rocky Mountain maple		x
<i>Amelanchier alnifolia</i> *	saskatoon serviceberry	x	
<i>Arctostaphylos uva-ursi</i>	bearberry	x	
<i>Berberis</i> spp.*	barberry		x
<i>Ceanothus fenderli</i>	Fendler ceanothus	x	
<i>Cercocarpus montanus</i> *	true mountainmahogany	x	
<i>Fallugia paradoxa</i> *	Apacheplume	x	
<i>Gutierrezia</i> spp.	snakeweed	x	
<i>Jamesia americana</i>	cliff jamesia	x	
<i>Juniperus communis</i> *	common juniper		x
<i>J. monosperma</i>	one-seed juniper	x	
<i>Philadelphus</i> spp.	mockorange	x	
<i>Phoradendron</i> spp.	mistletoe	x	x
<i>Picea engelmannii</i> *	Engelmann spruce		x
<i>P. pungens</i>	blue spruce	x	x
<i>Pinus edulis</i>	pinyon	x	

Appendix A. (continued).

Botanical name	Common name	Location	
		BNM	VSA
<i>P. flexilis</i> *	limber pine		x
<i>P. ponderosa</i> *	ponderosa pine	x	x
<i>Populus tremuloides</i> *	quaking aspen	x	x
<i>Potentilla fruticosa</i>	shrubby cinquefoil		x
<i>Pseudotsuga menziesii</i>	Douglas-fir	x	x
<i>Quercus gambelii</i> *	Gambel oak	x	x
<i>Q. undulata</i> *	wavyleaf oak	x	
<i>Ribes cereum</i>	wax currant	x	
<i>Robinia neomexicana</i>	New Mexico locust	x	
<i>Salix</i> spp.*	willow		x
<i>Shepherdia</i> spp.*	buffaloberry		x
<i>Yucca</i> spp.	yucca	x	

^aPlant names follow Nickerson et al. (1976).

^bBNM = Bandelier National Monument; VSA = Valle San Antonio.

^cIncludes grasses and grasslike plants.

^dNot submitted as voucher specimen, but common in area.

Appendix B. Vegetation sampling on the La Mesa burn, Bandelier National Monument.

METHODS

Vegetation in sites of various burn intensities was sampled on Bandelier National Monument during September-October 1980. Limited access in the Valle San Antonio during this time precluded sampling there. In order to compare results with data obtained previously, 5 of 6 plots sampled were identical to plots sampled during a post-fire study in fall 1977 (for description and locations of plots, see Foxx and Potter 1978: 28-30, 62-65, 87-88, 186-189). Sampling areas included those where forage samples were collected for nutritional analysis and were identified from telemetry studies as areas frequently used by elk in winter (Weber 1981, White 1981).

Plots were 20 x 50 m and were located in ponderosa pine habitats. Two plots were sampled in each of the following fire categories: severe, with tree crowns completely consumed; moderate, with only partial crown damage; and light, with the majority of trees alive and only light scorching of litter and duff.

Fifty 5 x 5-dm quadrats were systematically sampled for herbaceous vegetation in each plot. Shrub quadrats were 2 x 1 m and also totaled 50 per plot. Data recorded included percent canopy cover and frequency of occurrence for grass and browse species; forbs were combined in a single category. Percent canopy cover was measured using canopy coverage classes (Daubenmire 1959) and only live matter was recorded.

Appendix B. Percent canopy cover and frequency of occurrence of plants on the La Mesa burn in Bandelier National Monument, northern New Mexico, in fall 1980.

Species	Light ^a						Moderate						Severe					
	III-X ^b			III-2			II-1			II-2			II-3			III-4		
	\bar{x}	SD	F ^c	\bar{x}	SD	F	\bar{x}	SD	F	\bar{x}	SD	F	\bar{x}	SD	F	\bar{x}	SD	F
Graminoids^d																		
<i>Agropyron trichycaulum</i>	2.4	5.4	24	6.7	11.7	42	T		4	9.8	15.9	44	27.5	17.8	100	21.3	17.8	84
<i>Blepharoneuron tricholepis</i>				T		2										T		2
<i>Bouteloua gracilis</i>							6.9	8.4	62	8.2	12.8	44						
<i>Bromus</i> spp.	T ^e		6															
<i>Carex</i> spp.	4.0	7.4	46	T		4										T		8
<i>Festuca ovina</i>	1.6	4.2	22	5.1	9.8	36						12	7.1	11.1	54	18.0	13.2	92
<i>F. thurberi</i>				T		2	1.3	8.9	2									
<i>Koeleria cristata</i>	T		2				1.8	6.4	14	T		4						
<i>Muhlenbergia montana</i>	1.9	6.5	14	2.6	9.6	22				T		6	T		4	T		2
<i>M. wrightii</i>				T		6							2.5		20	T		8
<i>Poa</i> spp.				T		4												
<i>Sitanion hystrix</i>	T		12	T		6	6.0	8.5	46	T		4						
Other grasses	T		14	T		22	T		12	1.2		18	T		8	T		6
Total, graminoids	11.5		80	17.2		80	17.2		84	21.5		96	38.1		100	41.0		100
Forbs	1.7	2.4	56	2.2	5.8	32	23.2	15.1	100	14.7	12.0	90	4.8	5.5	88	T	1.1	26
Trees and shrubs																		
<i>Ceanothus fendleri</i>													1.1	5.8	6	T		2
<i>Cercocarpus montanus</i>													T		2			
<i>Juniperus monosperma</i>				T		2												
<i>Quercus gambelii</i>	T		2	T		2				1.9	9.3	8	3.5	12.5	8	T		8
<i>Robinia neomexicana</i>	T		4	T		2												
<i>Populus tremuloides</i>	T		2															
Other trees and shrubs				3.3	7.7	4												
Total, trees and shrubs	1.0		8	3.9		10				1.9		8	5.0		16	T		10
Total	14.1		92	23.3		84	40.4		100	38.1		100	47.9		100	42.5		100

^aRefers to fire intensity; see text for description.

^bPlot numbers follow Foxx and Potter (1978), except III-X, which was not sampled in 1977.

^c% frequency of occurrence.

^dIncludes grasses and grasslike plants.

^eLess than 1.0% cover.

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