ASSESSING WINTER DIETARY QUALITY IN BIGHORN SHEEP VIA FECAL NITROGEN

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Abstract: Fecal indicators of nutritional status of wild ungulates are less constrained than blood or urine analyses. Thus, we assessed the potential for fecal nitrogen concentration to predict winter dietary quality for Rocky Mountain bighorn sheep (*Ovis canadensis*) in Wyoming. Dietary nitrogen concentration and percent in vitro dry matter digestibility increased linearly with increases in fecal nitrogen concentration for hand-plucked diets of wild sheep on 4 winter ranges and for tannin-free diets fed to 3 penned adult female bighorn sheep (2 were ⅛ mouflon [*O. orientalis*]). A linear regression developed from field samples gathered in 2 winters accurately predicted winter dietary nitrogen concentrations using fecal nitrogen levels from other winters. Fecal nitrogen concentrations differed ($P < 0.0001$) among 7 winter ranges. Our data suggest that fecal nitrogen concentrations <1.3% may identify winter diets that are deficient in protein and energy for bighorn sheep.

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Wildlife managers desire reliable indicators of nutritional status of free-ranging ungulates to assess relationships between habitats and populations. One common method estimates quality of ungulate diets by analyzing nutritional quality of forage samples; however, indiscriminately collected forage samples underestimate nitrogen concentrations in ingested forage (Schwartz and Hobbs 1985). Other techniques include fecal indicators of dietary quality (Wofford et al. 1985, Leslie et al. 1989), blood analysis (Seal et al. 1972), and urinary analysis (DelGuidice and Seal 1988, DelGuidice et al. 1989). Use of the latter technique is limited to periods of snow cover, and blood analyses require capturing animals. Fecal indicators are not so constrained, and may be more useful.

Nitrogen is the most common constituent of feces used to assess dietary quality, and is positively correlated with diet digestibility, lignin (Erasmus et al. 1978), dietary protein (Holechek et al. 1982, Wofford et al. 1985), and change in mass (Gates and Hudson 1981, Hebert et al. 1984). However, Hobbs (1987) noted that undesirable statistical properties of predictive equations, including little within-season variation, may preclude precise estimates of dietary quality from fecal nitrogen concentration. Also, the presence of condensed tannins in some dicotyledonous forages increases the concentration of nitrogen in feces (Robbins et al. 1987). Leslie and Starkey (1987) defended the fecal nitrogen technique, contending that a significant difference between within-season fecal nitrogen estimates for 2 populations in similar habitats reflects a real difference in dietary quality. Further, tannins are virtually absent from cured grasses (McLeod 1974), and when grasses comprise most of the ruminant diet, fecal nitrogen and fecal dry matter digestibility appear closely associated with dietary nitrogen concentration and dietary dry matter digestibility, respectively (Holechek et al. 1982).

We examined the potential for fecal nitrogen concentration to assess dietary quality for Rocky Mountain bighorn sheep, which primarily eat cured grasses in winter. We tested null hypotheses that dietary dry matter digestibility and dietary nitrogen were not correlated with fecal nitrogen concentration; that relationships among fecal nitrogen concentration, dietary nitrogen concentration, and dry matter digestibility were the same for wild bighorns as for penned animals; and that mean fecal nitrogen levels did not differ among sheep populations on similar winter ranges.

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Table 1. Percent nitrogen and in vitro dry matter digestibility (SE) of 4 diets fed to captive Rocky Mountain bighorn sheep at the Sybille Wildlife Research Station, Wyoming, spring 1988.

Trial no.	Diet composition	Nitrogen %	Nitrogen SE	Digestibility %	Digestibility SE
1	Intermediate wheatgrass (*Agropyron intermedium*)	0.86	0.02	41	1.30
2	Smooth brome (*Bromus inermis*)	1.33	0.02	48	1.50
3	Smooth brome	1.89	0.04	52	0.66
4	Bluebunch wheatgrass/King spikefescue (*Leucopoa kingii*)	2.98	0.07	66	1.22

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STUDY AREAS AND METHODS

Controlled Diet Experiment

The protein availability of hays and pelleted diets that do not contain tannins can be used as a basis for understanding protein availability in tannin-containing diets (Robbins et al. 1987). Thus, we conducted experiments with penned animals that were fed tannin-free diets to check that fecal nitrogen-diet quality relationships for wild sheep were not influenced significantly by relatively tannin-free diets. From 28 April through 2 June 1988, we fed 4 diets ad libitum to 3 penned adult female mountain sheep at the Sybille Wildlife Research Station, operated by the Wyoming Game and Fish Department. Two of the sheep were ⅛ mouflon × ⅞ Rocky Mountain bighorn crosses. Diets were restricted to hand-clipped grasses and grass hays (Table 1) that were chopped into 3- to 4-cm fragments to discourage selective feeding. We assumed such diets would not contain tannins, because grasses contain virtually no tannins (Hobbs 1987, Robbins et al. 1987). Sheep were maintained outdoors in 10- × 20-m pens, each of which contained a concrete floor and a shed that provided protection from weather.

All trials consisted of a 10-day feeding period followed by fecal collection on the 11th day. During the first 2 trials, all sheep were housed together and fed the same diet (0.86% and 1.33% N, respectively). In the third trial, 2 sheep were housed together and fed a diet averaging 1.89% N (Table 1). Concurrently, the third sheep was housed separately and fed the highest quality diet (2.98% N), comprising the fourth trial. Sheep were separated into individual pens for fecal collections, where all pellet groups voided during 0800–1700 hours were collected and bagged separately, providing 3–5 fecal samples/sheep per trial. Nitrogen estimates from the 3–5 samples were pooled, resulting in 9 total FN estimates for statistical analysis. However, 1 sheep developed diarrhea near the end of the first trial, reducing our sample size to 8.

Wild Sheep Studies

We collected fecal droppings from bighorn sheep at 7 winter ranges and estimated diet quality at 4 of the 7 winter ranges, which were comprised primarily of big sagebrush (*Artemisia tridentata*)-steppe communities. Three of the winter ranges were located in northwestern Wyoming, including the Southfork of the Shoshone River, Camp Creek, and Whiskey Basin. The other four were in southcentral Wyoming, including Encampment River, Douglas Creek, A Bar A, and Bennett Peak.

Smith (1988), Arnett (1990), Cook (1990), and McWhirter (1993) determined food habits for bighorns in the study areas. Estimates of the proportions of sheep diets that contained tannins were made following Gibbs (1974), who listed plant families whose species do and do not contain tannins, and using data in Cook (1990), who

Table 2. Field data collections at Rocky Mountain bighorn sheep winter ranges, Wyoming, 1985–90.

Winter range	Diet samples		Fecal samples		Years of collection
	Method[a]	No./month	Method[a]	No./month	
Southfork Shoshone River	BC	≥16	Comp.	>16	1985–90
Camp Creek	BC	≥16	Comp.	≥16	1987, 1988
Whiskey Basin	Not sampled		Comp.	≥16	1987, 1988
Bennett Peak	FS	8–10	Indiv.	20–30	1986, 1987
Douglas Creek	FS	8–10	Indiv.	20–30	1986, 1987
Encampment River	Not sampled		Indiv.	20–30	1987, 1988
A Bar A	Not sampled		Indiv.	20–30	1986, 1987

[a] BC = bite count; FS = feeding site; Comp. = composite; Indiv. = individual.

determined tannin concentrations of 6 shrubs and 12 forbs from 3 of the study areas. Grasses and sedges comprised >50% of the diets in most months (Appendix). Graminoids and dicots with low amounts of tannins comprised >90% of the winter (late Nov–Mar) diets of bighorn sheep occupying these areas. Grasses important in bighorn diets in each area included bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), Sandberg's bluegrass (*Poa sandbergii*), and prairie Junegrass (*Koeleria cristata*). Sheep frequently browsed shrubs that contain few tannins, primarily big sagebrush, more often in March and during periods of deep snow. On 2 winter ranges where spring food habits data were available, use of tannin-containing species tended to increase with initiation of new growth.

We estimated dietary quality of wild bighorns at Southfork of the Shoshone River, Camp Creek, Bennett Peak, and Douglas Creek (Table 2). We used the bite count method to simulate botanical composition of diets at Southfork Shoshone River and Camp Creek, and subsequently determined chemical concentrations of estimated diets, because bighorn sheep on those ranges allowed us to observe them feeding at close range (<10 m). Diet composition estimated by the bite count method and subsequent determination of chemical concentration of simulated diets yields results similar to fistula sampling (Wallace et al. 1972). We hand-plucked the same parts of plants being eaten, or if the plant was consumed, we sampled plants adjacent to those fed upon by the sheep (Hobbs et al. 1983, Seip and Bunnell 1985, Goodson et al. 1991). We gathered enough forage (50 g/sample) to analyze chemical concentration of ≥16 simulated diets monthly from October or November through May.

We estimated quality of bighorn sheep diets at Douglas Creek and Bennett Peak using a slightly different method (Table 2), because those sheep generally avoided humans at close range. There, we used binoculars or spotting scopes to observe sheep feeding within 50–100 m, and we carefully identified locations and specific portions of plant communities where sheep fed. Diet composition was subsequently determined using the feeding site method (Cole 1956, Edge et al. 1988). Forage samples for nutrient analyses were clipped in the same proportions as observed at the feeding site and assembled into 8–10 simulated diets each month from December 1986 through December 1987 (except Mar–May).

For the 3 herds in northwestern Wyoming, we collected ≥16 fecal pellet samples/month (Table 2), each composite sample consisting of ≥10 pellets from 6–10 fresh fecal piles. At Douglas Creek, A Bar A, Bennett Peak, and Encampment River, 20–30 entire pellet groups were collected each month for each herd and analyzed separately. Composite diet (Hobbs et al. 1981) and fecal samples (Jenks et al. 1989) produce virtually identical means and SEs as individual samples.

Laboratory Analyses

Fecal samples were allowed to air dry, because air-drying has no effect on nitrogen concentration of feces (Jenks et al. 1990). Then, feces were oven-dried at 65 C for 24 hours and ground in a Wiley mill to pass through a 1-mm sieve. Percent fecal nitrogen and dietary nitrogen were determined using the macro-Kjeldahl technique (Horwitz 1980), analyzing 2–3 replicates/sample. Percent in vitro dry matter digestibility of diet samples was determined by the 2-stage method of Tilley and Terry (1963),

Table 3. Regressions of percent diet nitrogen and in vitro dry matter digestibility on percent fecal nitrogen of Rocky Mountain bighorn sheep in Wyoming, 1985–90.

	n	Intercept	SE	slope	SE	$S_{y \cdot x}$	P	r^2
Diet nitrogen vs. fecal nitrogen								
Penned animals	8	−0.36	0.36	1.31	0.23	0.25	0.0018	0.82
Field samples	16	−0.31	0.14	1.04	0.11	0.10	0.0000	0.87
Dry matter digestibility vs. fecal nitrogen								
Penned animals	8	29.16	5.42	14.02	3.55	4.50	0.0076	0.72

using rumen fluid from a domestic steer fed native grass hay. In vitro dry matter digestibility provides an index to digestible energy (Holechek et al. 1982).

Statistical Analyses

For penned animals, we used simple linear regression to relate average dietary nitrogen and dry matter digestibility values for each diet to average fecal nitrogen estimates from each sheep. We used polynomial regression to check for nonlinear relationships.

For wild bighorns, we used simple linear regression to relate average monthly estimates of dietary nitrogen concentration to average monthly fecal nitrogen levels on the 4 winter ranges where we gathered dietary quality data. We confined our analyses for wild sheep to fecal and diet samples gathered in late November–March, when tannins were lowest in bighorn diets (Table 2). We initially used data from Camp Creek and Southfork Shoshone River that were gathered during the 1986–87 and 1987–88 winters; at Bennett Peak and Douglas Creek we used data from the 1986–87 winter. We used the resulting equation to predict average dietary nitrogen concentration at Southfork Shoshone River for the 1985–86, 1988–89, and 1989–90 winters and for October–December 1987 diets at Bennett Peak and Douglas Creek. We did not relate dry matter digestibility to fecal nitrogen concentrations for field samples, due to insufficient replication. Significant differences between regressions from the field samples and the penned animals were determined with a test of homogeneity of slopes and intercepts (F-test, $P \leq 0.05$), following Snedecor and Cochran (1980). Accuracy of the equation to predict dietary nitrogen from fecal samples of wild sheep was tested with a paired t-test. We used 1-way fixed effects ANOVA to test for differences in fecal nitrogen concentration among the 7 winter ranges.

RESULTS

Controlled Diets

Fecal nitrogen concentrations increased linearly with increases in dietary nitrogen concentrations for controlled feeding trials, and accounted for 82% of the variation in dietary nitrogen (Table 3). The intercept was not different from 0.0 ($t = 0.95$, 1 df, $P = 0.38$). A second-degree polynomial fit to those data did not increase the amount of explained variation in dietary nitrogen concentration ($r^2 = 0.87$, $P > 0.10$), and did not appreciably improve accuracy of predictions, based upon the standard error of estimates ($S_{y \cdot x} = 0.27$ vs. 0.30). Fecal nitrogen concentration also was linearly related to dry matter digestibility for penned sheep, and accounted for 72% of the variation in digestibility. A second-degree polynomial did not reduce the sum of squares ($r^2 = 0.78$, $S_{y \cdot x} = 4.00$, $P > 0.25$).

Simulated Diets

The temporal pattern of fecal nitrogen concentration over 5 winter–spring periods at the Southfork of the Shoshone River, and 1 each at Camp Creek, Douglas Creek, and Bennett Peak was similar to dietary nitrogen (Figs. 1A–G). With a few exceptions, fecal nitrogen levels nearly paralleled dietary nitrogen estimates from mid-October to March. Lowest levels of fecal nitrogen generally corresponded to the lowest estimates of dietary nitrogen, and were usually obtained in late February to early March. During a drought in 1988 that delayed spring growth, fecal nitrogen reflected delayed increases in dietary nitrogen, which did not rise until mid-April (Figs. 1C and G). Anomalous dietary nitrogen data from December through mid-January at Camp Creek apparently resulted from supplementary feeding of pelleted alfalfa; we excluded those data from the regression analysis. Dietary nitrogen data for Douglas Creek in January 1987 also were excluded from regression

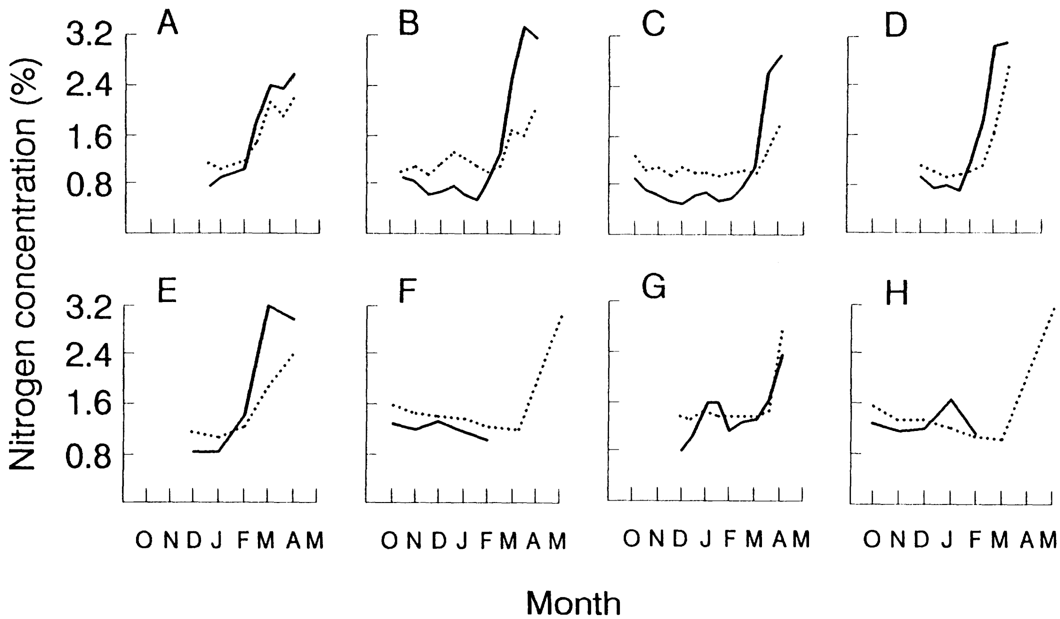

Fig. 1. Winter–spring values for percent fecal nitrogen (dotted lines) and dietary nitrogen (solid lines) for Rocky Mountain bighorn sheep on 4 winter ranges: Southfork Shoshone River, 1985–86 (A), 1986–87 (B), 1987–88 (C), 1988–89 (D), 1989–90 (E); Bennett Peak in 1987 (F); Camp Creek in 1987–88 (G); and Douglas Creek in 1987 (H).

analyses because field techniques were modified slightly after their collection.

Dietary nitrogen from the 4 winter ranges where we gathered diet quality estimates also increased linearly with increases in fecal nitrogen estimates, and the regression accounted for nearly 87% of the variance in estimates of dietary nitrogen concentration (Table 3). The slope and intercept did not differ from those for the regression developed from penned animals ($F = 4.09$; 1, 17 df; $0.05 \leq P \leq 0.10$; $F = 1.53$, $P > 0.25$). The regression equation from the 4 winter ranges accurately predicted dietary nitrogen concentration from fecal nitrogen concentrations from other years on the same ranges ($t = 0.36$, 13 df, $P > 0.692$; Table 4). Pooling data for all years across all winter ranges did not change the regression (percent dietary nitrogen = $-0.35 + 1.09$ percent fecal nitrogen; $S_{y \cdot x} = 0.09$, $r^2 = 0.88$; $F = 174.6$; 1, 23 df; $P = 0.0001$).

Comparisons Among Winter Ranges

Average winter fecal nitrogen levels differed among 4 winter ranges in the 1986–87 winter ($F = 32.75$; 3, 16 df; $P = 0.0001$), and among 7 winter ranges in the 1987–88 winter ($F = 9.80$; 6, 25 df; $P = 0.0001$), with lowest levels at the Southfork of the Shoshone River (Fig. 2). During the 1987–88 winter, A Bar A, Douglas Creek, and Encampment River winter ranges were associated with comparatively high levels of fecal nitrogen; Bennett Peak, Camp Creek, and Whiskey Basin exhibited intermediate values; and Southfork of the Shoshone River was associated with low values. Rankings from fecal nitrogen data corresponded well with data for the 4 winter ranges where we also estimated dietary nitrogen, and with the corresponding regressions from penned sheep; average winter estimates of dietary nitrogen were ±1 SE of the regression line (Fig. 3A). Average winter field-gathered estimates for dry matter digestibility did not correspond as well with predictions from the penned sheep, although trends were similar (Fig. 3B). Results indicated that sheep at Camp Creek and Bennett Peak consumed diets that were higher in dry matter digestibility than those at Southfork of the Shoshone River ($F = 3.01$; 3, 16 df; $P = 0.045$).

DISCUSSION

Regression analyses based upon penned animals fed tannin-free diets suggest that fecal nitrogen concentration might provide accurate assessments of protein and energy intake for free-ranging bighorn sheep that consume winter

Table 4. Fecal nitrogen (%) and observed and predicted[a] estimates of dietary nitrogen (%) during winter for Rocky Mountain bighorn sheep in Wyoming, 1986, 1987, 1989, 1990.

Winter range	Date	Fecal N	Dietary N Predicted	Dietary N Observed	Difference
Southfork Shoshone River[b]	Jan 1986	1.00	0.73	0.94	−0.21
	Jan 1986	1.09	0.82	0.75	0.07
	Jan 1989	1.05	0.78	0.78	0.00
	Jan 1989	0.96	0.69	0.79	−0.10
	Feb 1989	0.99	0.72	0.74	−0.02
	Feb 1989	1.29	1.03	1.01	0.02
	Jan 1990	1.10	0.83	0.81	0.02
	Feb 1990	1.04	0.82	0.79	0.03
Douglas Creek	Oct 1987	1.58	1.33	1.33	0.00
	Nov 1987	1.55	1.30	1.07	0.23
	Dec 1987	1.47	1.22	1.07	0.15
Bennett Peak	Oct 1987	1.55	1.30	1.28	0.02
	Nov 1987	1.44	1.19	1.26	−0.07
	Dec 1987	1.39	1.36	1.36	0.00

[a] Percent dietary nitrogen = 1.04 fecal nitrogen −0.31, $s_{y \cdot x}$ = 0.10.
[b] Fecal nitrogen and dietary nitrogen estimates were made twice/month at Southfork Shoshone River and once/month at Bennett Peak and Douglas Creek.

diets that are low in tannins. Indeed, dietary nitrogen of free-ranging bighorns was a highly predictable function of fecal nitrogen in midwinter. We based that conclusion upon the standard error of the estimate ($S_{y \cdot x}$ = 0.09) from pooled samples, and the ability to predict dietary nitrogen accurately for samples gathered in other years on the same ranges. Accuracy of dry matter digestibility predictions was lower, probably a result of wider variance in field samples compared with controlled diet samples. Over the range of values in our study, linear relationships existed between fecal nitrogen and dietary nitrogen concentration and between fecal nitrogen and dry matter digestibility. Finally, our data support Leslie and Starkey's (1987) contention that a significant difference between within-season fecal nitrogen estimates for different populations in similar habitats reflects a real difference in dietary quality.

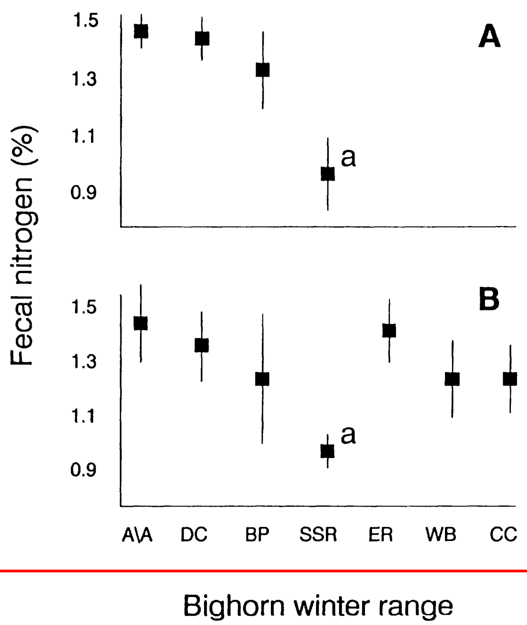

Fig. 2. Average November to mid-March fecal nitrogen (%) values for 4 bighorn sheep winter ranges in 1986–87 (A) and for 7 winter ranges in 1987–88 (B). Vertical bars indicate 1 SE. Points followed by letters differ ($P < 0.05$) from others in same year. A/A = A Bar A; DC = Douglas Creek; BP = Bennett Peak; SSR = Southfork Shoshone River; ER = Encampment River; WB = Whiskey Basin; CC = Camp Creek.

Wofford et al. (1985) reviewed studies that showed that fecal nitrogen-dietary quality associations deteriorate when dietary nitrogen levels are >2.4% nitrogen (15% crude protein). Such a relationship is demonstrated by data from mid-March to May (Fig. 1), suggesting a nonlinear relationship between fecal nitrogen and dietary nitrogen concentrations may occur at high dietary nitrogen levels (Stallcup et al. 1975, Putman and Hemmings 1986). From late November through early March, dietary nitrogen concentrations in our winter study areas were <2.4%, dietary tannin levels were low, and fecal nitrogen levels tracked changes in dietary nitrogen concentrations rather closely. Also, our regression was similar to that of Wofford et al. (1985) for cattle diets with <2.4% dietary ni-

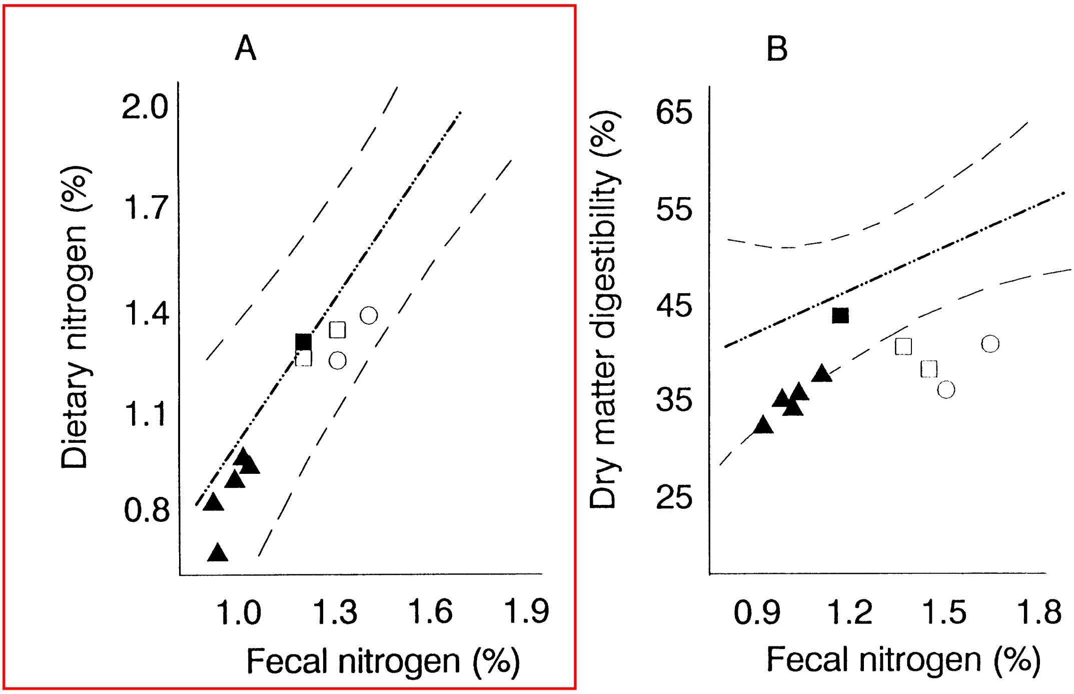

Fig. 3. Regression lines for penned bighorn sheep for (A) dietary nitrogen concentration against fecal nitrogen concentration (r^2 = 0.82, P = 0.0018); and (B) percent dry matter digestibility against fecal nitrogen concentration (r^2 = 0.72, P = 0.0076). Dashed lines indicate 95% confidence interval. Also, corresponding average values are plotted for November–February data from wild bighorn sheep on winter ranges: Southfork Shoshone River from 1985–86 to 1989–90 (solid triangles); Camp Creek in 1987–88 (solid square); Douglas Creek in 1986–87 and November–December 1987 (open circles); and Bennett Peak in 1986–87 and November–December 1987 (open squares).

trogen: $Y = -0.71 + 1.07$ fecal nitrogen, $S_{y \cdot x}$ = 0.07, suggesting a general relationship may exist among ungulates that consume diets with low tannin levels in winter.

Diet composition may influence whether or not fecal nitrogen concentrations provide a reliable tool for identifying nutritional deficiency among ungulates in general (e.g., Leslie and Starkey 1985, Wofford et al. 1985) or in seasons other than winter. Dietary quality assessments within or among herds may be confounded if ungulates consume diets containing condensed tannins (Robbins et al. 1987). Sheep herds in our study occupied relatively simple shrub-steppe communities, and primarily consumed grasses and several species of Asteraceae, none of which contain tannins (Hobbs 1987, Cook 1990); tannins do not appear important in protein availability of most deciduous winter browse (Robbins et al. 1987). Tannins were in <9% of diets consumed by bighorn sheep from December through March at the 7 winter ranges in our study. Selecting low-tannin diets might influence winter survival, because protein availability would be maximized at a time when the concentration of nitrogen in forage is lowest and weather is often harshest.

Empirical data from domestic sheep (Allden and Jennings 1969) and cattle (Wofford et al. 1985) suggest fecal nitrogen concentrations <1.7% correspond with summer diets of ≤6.6% crude protein, and indicate potential for nutritional deficiency via reduced forage intake. Winter diets ≤7% generally are considered submaintenance for ungulates (French et al. 1955, Mould and Robbins 1981, Natl. Res. Counc. 1985). Our data indicate that fecal nitrogen ≤1.3% corresponds with winter diets with ≤6.6% crude protein in bighorn sheep. Thus, winter fecal nitrogen concentrations <1.3% may indicate potential for nutritional deficiency via reduced intake within Rocky Mountain bighorn sheep herds in sagebrush–steppe winter ranges.

MANAGEMENT IMPLICATIONS

Fecal nitrogen concentration may aid in prioritizing winter-range improvement projects and in decisions for herd management or more-detailed evaluations of nutrition. Diet quality assessments should be limited to fecal collections made during late November–February, when ungulate diets may be low in tannins, and when nutritional deficiencies are likely to be most pronounced.

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Appendix. Percentage composition by vegetation classes and tannin content of Rocky Mountain bighorn sheep diets on winter ranges in Wyoming.[a]

Winter range Vegetation classes	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Southfork Shoshone River[bc]								
Graminoids				73		54	58	51
Forbs				6		14	14	41
Shrubs				21		33	28	8
Tannins				2		7	12	21
Southfork Shoshone River[de]								
Graminoids		54	88	94	88	84	86	85
Forbs		20	5	5	8	3	2	10
Shrubs		26	7	1	5	12	12	5
Tannins		7	2	0	1	5	3	6
Whiskey Basin[de]								
Graminoids		52	20	55	27	12	63	40
Forbs		21	44	20	16	12	16	35
Shrubs		27	36	25	57	76	21	24
Tannins		3	0	6	4	1	4	16
Camp Creek[de]								
Graminoids		7					51	
Forbs		15					2	
Shrubs		78					47	
Tannins		8					2	
Bennett Peak[cf]								
Graminoids	59	45	46	49	39			
Forbs	39	32	1	25	51			
Shrubs	2	23	52	25	9			
Tannins	0	19	4	9	0			
Douglas Creek[cf]								
Graminoids	45	59	58	38	86			
Forbs	54	25	30	47	12			
Shrubs	1	15	12	14	1			
Tannins	1	15	5	8	1			
Encampment River[eg]								
Graminoids		58	44	85	67	68		
Forbs		34	45	15	26	12		
Shrubs		8	11	0	7	20		
Tannins		5	0	0	4	0		

[a] Tannin content based on Gibbs (1974) and data in Cook (1990).
[b] Based on microhistological analysis of fecal fragments (Smith 1988).
[c] 1986–87.
[d] Based on microhistological analyses of fecal fragments (McWhirter 1993).
[e] 1987–88.
[f] Based on bite-count analyses (Cook 1990).
[g] Based on bite-count analyses (Arnett 1990).