NITROGEN METABOLISM IN ELK

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Abstract: Nitrogen metabolism of elk (*Cervus elaphus nelsoni*) was investigated during 15 feeding trials of single- and multiple-component rations. Endogenous urinary nitrogen was 0.16 g N/kg$^{0.75}$/day, metabolic fecal nitrogen was 5.58 g N/kg dry-matter intake, apparent nitrogen digestibility ranged from −99.9 to 88.0%, and true nitrogen digestibility was 98.0%. Feed nitrogen concentration was significantly related to fecal nitrogen content for phenolic-free rations. Ingested phenolics significantly increased fecal nitrogen excretion. Urea kinetic experiments were conducted in conjunction with 8 of the in vivo trials in which elk recycled 18–85% of the urea produced, which represented 23.9–198.0% of their dietary nitrogen intake. Biological value of dietary protein fell from 100 to 42% as dietary protein content increased from 5.6 to 29.3%. Digestible-energy intake necessary to maintain a positive nitrogen balance was 153 kcal/kb$^{0.75}$/day. Estimates of dry-matter intake needed to meet maintenance nitrogen requirements at varying dietary crude-protein concentrations are presented.

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As elk expand their range and numbers (Ward 1971), increased knowledge of elk nutritional requirements is essential for their management. Because data on the protein requirements of elk are insufficient, estimates of nitrogen requirements have been derived from studies of deer (*Odocoileus* spp.) and domestic livestock (Boll 1958, Schommer 1978, Westra 1978, Nelson and Leege 1980), even though digestive and metabolic capabilities can vary among species. Therefore, specific knowledge of elk requirements and the efficiencies of dietary use are necessary to avoid possibly misleading or inaccurate evaluations when using extrapolations from other species. Efficiencies of protein assimilation may be major determinants of survival and productivity of free-ranging elk because of the relatively low protein content of many winter feeds (Collins et al. 1978, Schommer 1978).

Maintenance requirements of an animal for absorbed nitrogen are determined by the addition of endogenous urinary nitrogen (EUN) and metabolic fecal nitrogen (MFN). EUN is the nitrogen lost in the urine from normal turnover of body nitrogen, and is traditionally defined as the minimum loss of nitrogen through the urine when consuming a nitrogen-free diet (Smuts 1935). MFN is the portion of the feces that is composed of microbial cells, mucus, and eroded cells of the gastrointestinal tract, and is often considered the nitrogen cost of the digestive processes (Folin 1905, Smuts 1935). True digestibility coefficients for plant nitrogen are generally high for ruminants, although variability can occur if soluble digestion inhibitors, such as phenolics, are present within the plant cells (McLeod 1974).

Because absorbed nitrogen can subsequently be used directly for productive processes or converted to urea in the liver, knowledge of urea kinetics may be important in understanding the total nitrogen economy. Urea recycling is the process whereby urea in the blood escapes urinary excretion and reenters the gastrointestinal tract. Recycled urea can serve both as a source of protein and as a buffer to the rumen microbial environment against dietary nitrogen deficiency (Houpt 1959, Waldo 1968). Urea that en-

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Table 1. Diets, diet composition, and nitrogen metabolism parameters of captive elk.

Diet	Elk (*N*)	Crude protein (% of dry matter)	Protein intake (g/day)	Apparent protein digestibility (%)	Nitrogen retention (g N/kg$^{0.75}$ /day)	Urea recycled (%)	Urea degradation (g N/kg$^{0.75}$ /day)	Plasma urea (mg/100 ml)
Alfalfa	4	17.6	318.4	70.6	−0.06	29.1	0.94	67.3
Bluegrass straw	3	3.9	63.2	−16.1	−0.61			
Brome	4	5.6	180.5	32.9	−0.11	66.3	0.82	35.8
Canarygrass	4	6.4	134.1	33.9	−0.31	49.6	0.86	56.3
Dried wheat grass	3	19.6	896.5	77.1	0.54			
Fireweed	3	12.0	351.6	16.1	−0.08	66.1	1.19	42.6
Fresh wheat	2	29.3	779.1	88.0	0.64	17.6	0.66	88.6
Maple leaves	4	3.8	69.5	−99.9	−0.61	51.9	0.74	43.0
Orchardgrass	3	6.2	160.5	47.2	−0.23	48.0	1.32	75.6
Timothy	4	7.6	258.7	37.3	0.03	85.3	1.98	29.1
Ration A	4	9.7	276.6	43.7	−0.11			
B	4	8.0	193.4	30.9	−0.22			
C	3	16.7	469.2	75.2	0.25			
D	3	12.0	446.4	69.2	0.14			
E	3	5.4	144.5	3.4	−0.47			

ters the rumen from the blood may diffuse directly across the rumen wall or enter via the saliva (McDougall 1948, Houpt 1959, Somers 1961*a*,*b*). Once in the rumen, urea is readily hydrolyzed by bacterial urease to produce carbon dioxide and ammonia. The ammonia may then either be reabsorbed and reconverted to urea in the liver, synthesized into bacterial protein, or excreted in feces. Recent studies using continuous infusion of several isotopes have resulted in conflicting estimates of the proportion of endogenous urea degradation that takes place in the rumen and in the lower gastrointestinal tract (Nolan and Leng 1972, Nolan and Stachiw 1979). If the recycled urea enters the lower gastrointestinal tract, the value of this phenomenon as a nitrogen-conserving mechanism will depend upon absorbability of nitrogen metabolites in the lower gut (Norton et al. 1978). Thus, we fed elk diets of differing protein concentrations to determine protein digestibility, nitrogen retention or biological values, maintenance nitrogen requirements, and the extent of urea recycling.

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METHODS

Eight elk at least 1 year old were fed 10 single-species diets (alfalfa, fresh and dried early-growth wheat herbage, canarygrass [*Phalaris canariensis*], maple leaves [*Acer* sp.], smooth brome, [*Bromus inermis*], orchardgrass [*Dactylis glomerata*], fireweed willow-herb [*Epilobium angustifolium*], timothy, Kentucky bluegrass straw [*Poa pratensis*] [Table 1]) and 5 mixed rations (Table 2) during April–September 1977 and March–July 1978. Mixed rations consisted of feeds fed in the single-species trials except ration C, which consisted of fresh bluegrass and 1st cuttings of a wild pasture composed primarily of quackgrass (*Agropy-*

Table 2. Composition of mixed experimental rations.

Ration	Constituent	Dry matter in total ration (%)
A	Maple leaves	33.24
	Timothy	33.33
	Alfalfa	33.43
B	Fireweed	33.78
	Orchardgrass	33.08
	Brome	33.14
C	Fresh bluegrass	13.96
	Fresh quackgrass pasture	86.04
D	Wheat herbage	21.52
	Canarygrass	22.53
	Fresh quackgrass pasture	49.80
	Fresh bluegrass	6.95
E	Idaho fescue	73.66
	Molasses	26.34

ron repens), and ration E, which consisted of Idaho fescue (*Festuca idahoensis*) and molasses, the latter necessary to increase palatability (Table 2).

Elk that were habituated to confinement were conditioned to the test ration for a 10-day pretrial period in 10 × 10-m outdoor graveled pens devoid of vegetation. During the 1st 5 days of the pretrial period the test ration was fed ad libitum until daily intakes could be predicted. Daily allotments of the test ration were then adjusted until no orts remained after 24 hours, and were divided into 2 feedings/day. Intake remained at slightly below ad libitum levels for the remaining 5 days of the pretrial and for the entire 7-day trial period when total urine and fecal collections were made. Water was available ad libitum.

Elk were immobilized at the completion of the pretrial period by using succinylcholine chloride, which has no effect on the measured blood parameters (Wesson et al. 1979). A 20-ml blood sample was drawn from either the saphenous or jugular vein before the animals were moved into 2.5 × 2.5-m metabolism crates (Cowan et al. 1969). If urea kinetics were to be determined, blood sampling was followed by an intravenous injection of approximately 150 μCi of ^{14}C-urea in 35 ml of sterile saline. Urine was subsequently collected every 2–8 hours for the next 24 hours. During the remaining trials urine was collected at least once every 24 hours, and a 250-ml sample was stored at −20 C for later analyses. Feces were dried at 100 C for 24 hours to determine total dry matter, and a small uncontaminated sample was fresh frozen to be used in subsequent analyses. Urine, fecal, and feed nitrogen were determined by Kjeldahl procedures, and energy by bomb calorimetry. All calculations were made on a 100% dry-matter basis.

Because of quenching difficulties encountered when measuring specific activity of urine mixed directly with scintillation cocktail, the carbon dioxide capture method of Robbins et al. (1974) was employed. Although it maintains a high collection and counting efficiency, this method is not subject to incidental differences in urine coloration. Specific activity was assayed with a Searle Isocap/300 liquid scintillation system, and counts were corrected for counting efficiency by the channels-ratio method. Urine and plasma urea concentrations were determined by the method of Foster and Hochholzer (1971).

The logarithmic decay curve of specific activity vs. time was extrapolated to zero time to estimate the specific activity immediately after injection. Because the exact times of each urination were not known, and because each sample could represent several urinations, the midpoint in time between urine collections was recorded as the time of urination. The initial urine collection was not included in this calculation because the time of the urination just preceding in-

jection was not known. Urea kinetic parameters were calculated according to the equations in Mugerwa and Conrad (1971) and Robbins et al. (1974). The method used to determine urea kinetic measurements assumes a rapid equilibration of the injected ^{14}C-urea with the urea pool of the animal, that urea metabolism is random, and that the experimental animals are in a metabolic steady state during the test period (Mugerwa and Conrad 1971).

RESULTS AND DISCUSSION

The crude-protein content of the feeds ranged from 3.8 to 29.3%, and daily consumption of protein varied from 63 to 896 g/day (Table 1); these levels are representative of the variability encountered for free-ranging elk (Schommer 1978, Nelson and Leege 1980). MFN determined as the intercept of digestible amount vs. dietary crude-protein concentration was 5.58 g N/kg dry-matter intake (3.49 g protein/100 g dry-matter intake) for elk consuming phenolic-free rations, and results in the curvilinear relationship between apparent protein digestibility and dietary crude-protein content (Fig. 1). MFN of elk is similar to the 5.3 g N/kg dry matter intake for white-tailed deer (*Odocoileus virginianus*) (Holter et al. 1979*a*), and within the ranges of 4.35–6.77 g N/kg dry-matter intake measured for sheep and 3.38–5.78 g N/kg dry-matter intake for cattle fed hay rations similar to those of this study (ARC 1965). EUN determined from the regressions of nitrogen intake or urea-nitrogen excretion on total urinary nitrogen excretion was 0.16 g N/kg$^{0.75}$/day, and is comparable to the 0.13–0.19 g N/kg$^{0.75}$/day values calculated for cattle of similar weight and maturity (ARC 1965). However, EUN for elk is higher than those reported for other wild ungulates, including 0.09 g N/kg$^{0.75}$/day for red deer (*Cervus elaphus*) (Maloiy 1968), 0.08 g N/kg$^{0.75}$/day for roe deer (*Capreolus capreolus*) (Eisfeld 1974), and 0.11 g N/kg$^{0.75}$/day for white-tailed deer (Robbins et al. 1975).

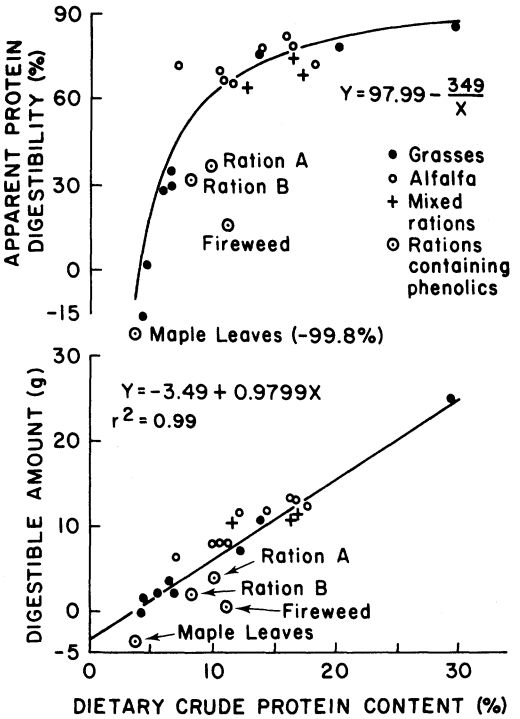

Fig. 1. Apparent protein digestibility and digestible amount (apparent protein digestibility × dietary crude protein) in elk as a function of dietary crude-protein content. Diets containing fireweed and maple leaves were not included in the regressions because of their high phenolic content, but are included in the graph for comparison. Data from Thorne (unpubl. reps., Wyo. Fish and Game Comm., 1968, 1973) and Westra (1978) are included.

Apparent protein digestibilities ranged from −99.9% for maple leaves to 88.0% for fresh spring-wheat herbage (Table 1). Negative apparent digestibilities are possible when metabolic fecal excretion exceeds absorbed dietary intake. Feeds containing crude protein concentrations below 3.56% (metabolic fecal nitrogen [3.49]/true protein digestibility [0.98]) will result in negative apparent protein digestibilities for elk (Fig. 1). True pro-

tein digestibility is an estimate of the percentage of the forage protein ingested that is actually absorbed, and was 98.0% for elk, using the combined data of this study and that recalculated from Westra (1978) and Thorne (unpubl. reps., Wyo. Fish and Game Comm., 1968, 1973) (Fig. 1). If fresh spring-wheat herbage is omitted from the regression because it is conspicuously higher in protein content than the other feeds, the recalculated equation is $Y = -3.54 + 0.97X$ ($R^2 = 0.96$), which is not markedly different from that using all data points. True nitrogen digestibility for elk is slightly higher than the 84.4–95.7% for white-tailed deer (Robbins et al. 1974, Smith et al. 1975, Holter et al. 1979*b*) and 96.0% for red deer (calculated by Robbins [1973] from the data of Maloiy [1968]). Although many of the values calculated for true nitrogen digestibility for domestic ruminants are slightly lower than values for wild ruminants (Knight and Harris 1966, Ford and Milligan 1970, Wales et al. 1972), the differences may be due to varying metabolic fecal losses, to experimental procedures, or to quality and condition of feeds rather than to species differences in efficiency of nitrogen use.

A group of secondary plant compounds collectively called phenolics can form irreversible complexes with proteins and thereby reduce protein digestibility once released from plant cell vacuoles during mastication. Phenolics may specifically reduce apparent protein digestibility by complexing with and precipitating dietary and microbial proteins in the rumen and by interfering with the permeability of the intestinal wall by forming complexes with protein of epithelial cells (McLeod 1974). Plants commonly consumed by free-ranging elk contain phenolics, especially in winter when a large proportion of the elk's diet consists of browse (Hanks et al. 1971, Schommer 1978). Fireweed, maple leaves, and the mixed rations containing these forages (rations A and B) contain significant levels of condensed and hydrolyzable phenolics (Mould and Robbins, unpubl. data). The apparent protein digestibilities of these rations were from 11 to 70% of the predicted values at the same protein content as the phenolic-free rations (Fig. 1). Because of the profound effect that phenolics had upon protein use by elk, these rations were not included in the digestibility regressions. Their inclusion markedly increases the MFN estimate, and may increase true nitrogen digestibility above the theoretical maximum of 100% (Van de Veen 1979).

Comparisons of fecal nitrogen content with feed nitrogen content have recently been investigated as possible indices of the nitrogen status of wildlife populations, including free-ranging elk (Gates and Hudson 1979). Fecal nitrogen content for elk was correlated ($P < 0.01$) with feed nitrogen content for rations containing low levels of phenolics (Fig. 2). These data are consistent with those for several East African herbivores in which feed nitrogen concentration was found to be affected by dietary type and crude-protein concentration (Arman et al. 1975). Although significant regressions have been generated from data for fecal samples from animals fed grasses and legumes, extrapolations to browses and forbs that may contain soluble phenolics could be inaccurate. Fecal nitrogen concentration was elevated in trials using phenolic-containing species, because of the protein-complexing capabilities of phenolics (Fig. 2). This observation, coupled with the prevalence of phenolic-containing plants (Rhodes and Cates 1976), seriously limits the simple use of fecal nitrogen content as an indicator of

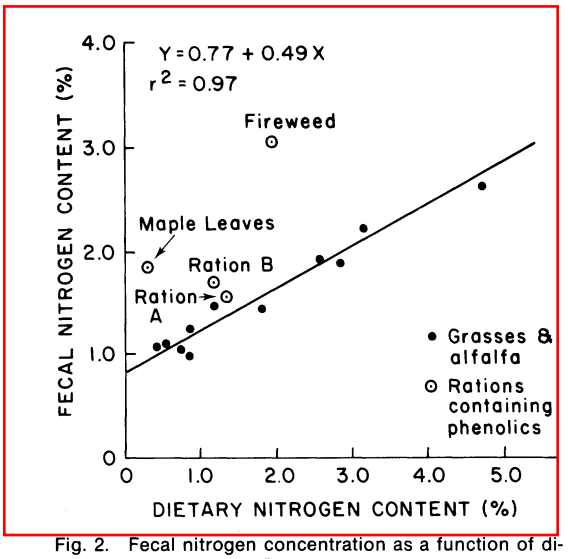

Fig. 2. Fecal nitrogen concentration as a function of dietary nitrogen content. Diets containing fireweed and maple leaves were not included in the regression because of their high phenolic content, but are included in the graph for comparison.

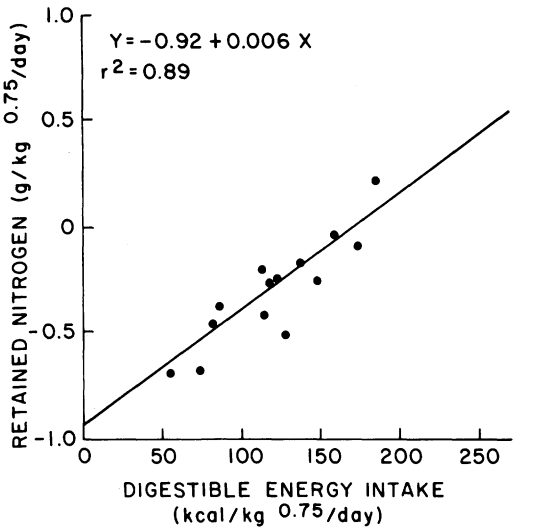

Fig. 3. Nitrogen retained by elk at various levels of digestible-energy intake.

dietary nitrogen concentration for herbivores.

Total nitrogen economies of the elk apparently were affected by several variables simultaneously. In addition to the efficiency of nitrogen absorption and use, energy intake is an important consideration because animals catabolize dietary and body fats and proteins to meet energy requirements when dietary energy is deficient. Additionally, animals consuming protein in excess of their nitrogen requirement, but deficient in energy, may not retain dietary nitrogen as efficiently, because sufficient carbon substrates would not be available for microbial amino acid synthesis (Belasco 1954). Digestible-energy intake in excess of 153.3 kcal/kg$^{0.75}$/day was necessary for the elk to maintain a positive nitrogen balance (Fig. 3). The estimated digestible-energy requirement for elk to maintain nitrogen balance is within range of 153–160 kcal/kg$^{0.75}$/day determined for maintenance of white-tailed deer (Ullrey et al. 1969, 1970; Holter et al. 1977).

Urea degradation by elk ranged from 0.66 to 1.98 g N/kg$^{0.75}$/day (Table 1), which is generally higher than the range (0.47–1.18) observed by Westra (1978). The percentage of urea recycled by elk was highly variable, ranging from 17.6% for fresh wheat herbage to 85.3% for timothy. The amounts of urea recycled in elk are comparable to those determined for other ruminants: 0.34–0.66 g N/kg$^{0.75}$/day for caribou (*Rangifer tarandus*) (Wales et al. 1972), 0.45–1.38 g N/kg$^{0.75}$/day for white-tailed deer (Robbins et al. 1974), 1.17–1.99 g N/kg$^{0.75}$/day for cattle (Mugerwa and Conrad 1971), and 0.05–0.59 g N/kg$^{0.75}$/day for sheep (Cocimano and Leng 1967, Ford and Milligan 1970, Nolan et al. 1976).

Because a large proportion of the total urea pool is contained in and enters the gut through the blood (Mazanov and Nolan 1976), close correlations of urea kinetic parameters to plasma urea concentration were expected. Urea-nitrogen excretion rate, urea pool size, and urea entry rate were all correlates ($P < 0.01$) of plasma urea concentration (Fig. 4).

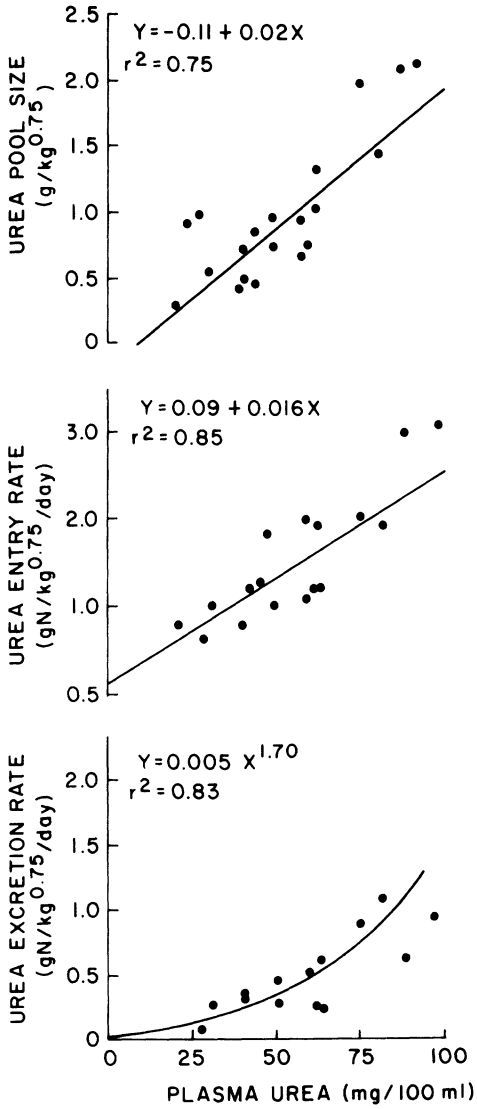

Fig. 4. Relationships of urea pool size, urea entry rate, and urea excretion rate to plasma urea in elk.

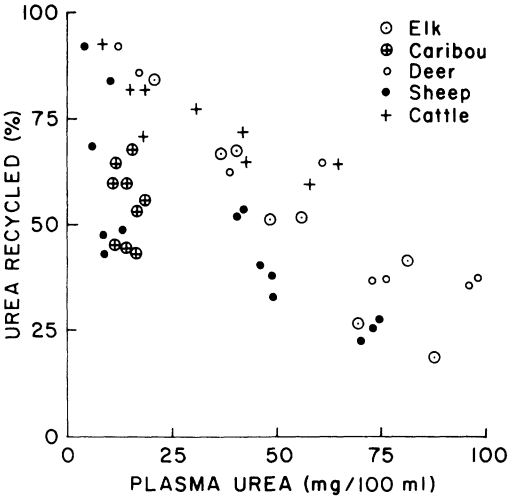

Fig. 5. Percentage of recycled urea at various plasma urea concentrations in sheep (Cocimano and Leng 1967), cattle (Mugerwa and Conrad 1971), white-tailed deer (Robbins et al. 1974), caribou (Wales et al. 1972), and elk.

Changes in urea entry rate, whether from endogenous or dietary sources, are reflected by plasma urea, which in turn is a determinant of urinary urea excretion (Schmidt-Nielsen and Osaki 1958, Somers 1961*a*, Norton et al. 1978). The curvilinearity of the relationship between urea-nitrogen excretion rate and plasma urea is probably a result of increased filtering capacity of the kidneys at higher levels of plasma urea concentrations (Hill 1976).

Degradation rate is assumed to represent the urea that reenters the digestive tract and is hydrolyzed by gastrointestinal microflora. Although the amount of urea entering the gastrointestinal tract of sheep correlated with the plasma urea concentration (Houpt and Houpt 1968, Norton et al. 1978), similar correlations were not significant in either this study or a study of urea kinetics in white-tailed deer (Robbins et al. 1974). This observation could mean that direct diffusion of urea across the gut in elk is not simply a function of plasma urea concentration, as it is for sheep, or that urea entry indirectly through the saliva is quantitatively more important in elk than in sheep.

The potential for conserving nitrogen by urea recycling appears to be substantial. Recycled nitrogen as a percentage of dietary nitrogen intake ranged from 23.9% for elk fed alfalfa to 198.0% for

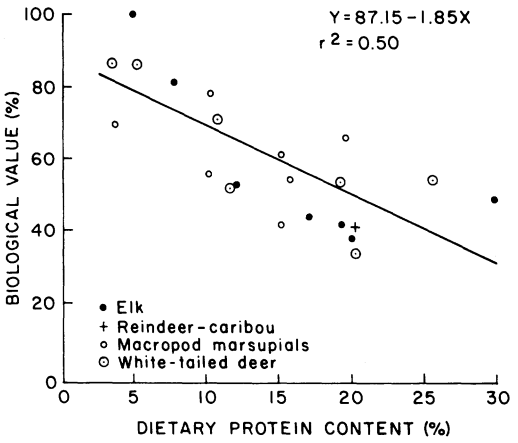

Fig. 6. Proportion of absorbed dietary protein used for tissue production (biological value), as a function of dietary content in elk, reindeer-caribou (McEwan and Whitehead 1970), macropod marsupials (Hume 1977, Kennedy and Hume 1978), and white-tailed deer (Ullrey et al. 1967, Robbins 1973).

maple-leaf diets. Elk that recycled urea nitrogen in excess of their intake were apparently mobilizing and recycling tissue nitrogen. Urea recycling studies of all species except caribou show that recycling as a percentage is highest when plasma urea concentrations are the lowest (Fig. 5). However, Norton et al. (1978) cautioned against the presumption that high levels of urea recycling imply greater nitrogen efficiency because carbon substrates must also be available for net protein synthesis. In addition, recycled urea can be as much a result of endogenous protein catabolism as of conservation of dietary nitrogen. Therefore, high levels of recycled urea may be incidental to the overall nitrogen economy of the animal when the urea pool is flooded by nitrogen from catabolized body proteins, rather than an effective nitrogen-conserving mechanism. However, maintenance of a viable rumen microbial population is essential to insure digestive capabilities throughout periods of nutritional deficiency (DeCalesta et al. 1974), and recycled urea is a significant nitrogen source for the rumen environment (Houpt 1959) when dietary sources are low.

Biological values of absorbed dietary nitrogen for elk were determined by using in vivo trials in which elk were fed energy above their estimated maintenance requirement (Mitchell 1924). Biological value decreased from 100 to 42% as dietary crude protein increased from 5.6 to 29.3%, which is consistent with biological values of ingested protein for other ruminants and macropod marsupials (Fig. 6). The decrease in biological value may result from less efficient use of dietary protein with increasing urea production, reduced urea recycling (Fig. 5), and increased urea excretion (Fig. 4).

The maintenance requirement of elk for dietary protein is a dynamic function involving digestibility and biological value of dietary nitrogen, metabolic weight of the animal (EUN), and dry-matter intake (MFN). Though EUN is a constant function of metabolic body weight, the nitrogen intake necessary to meet the MFN requirement varies with dietary crude-protein concentration, because as the crude protein of the ingesta decreases, the required dry-matter intake for nitrogen balance necessarily increases. Predicted minimum dry-matter intakes required by elk to meet their maintenance nitrogen requirements were determined at various dietary protein concentrations by using the computer program diagrammed in Fig. 7. Required dry-matter intake of feeds increases sharply as the dietary protein concentration decreases below 8% (Fig. 8). It is apparent that the larger the animal, the greater the required dry-matter intake to meet maintenance nitrogen requirements, as a result of increased EUN and concomitant increase in MFN. When dietary crude-protein concentration is equal

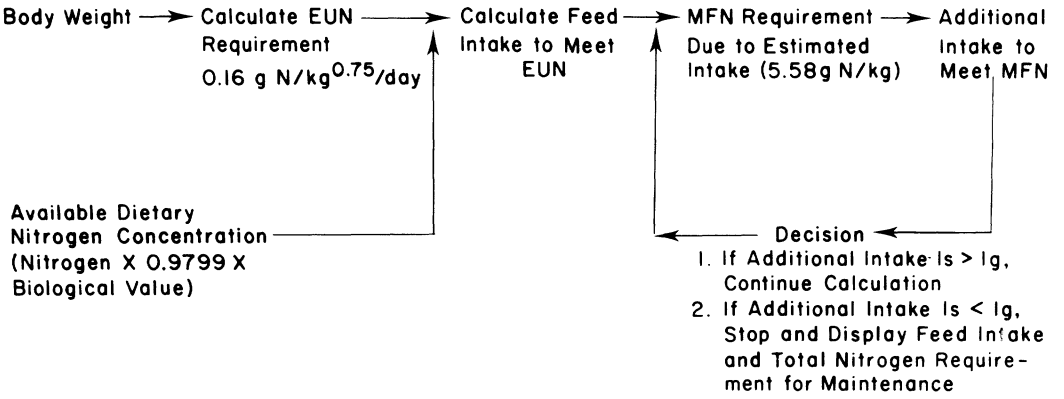

Fig. 7. Flow chart for calculating dry-matter intake needed by elk to meet the maintenance nitrogen requirements at various dietary nitrogen concentrations.

to or less than the MFN as a percentage of dry-matter intake (3.49% for elk), it is not possible for an animal to meet its maintenance nitrogen requirement because dietary nitrogen intake cannot exceed the losses in MFN.

Maximum dry-matter ingestion rates of elk in captive conditions have ranged from 2.6 and 3.3% of body weight/day when fed high-quality grass and alfalfa hay (Hungerford 1952, Robbins et al. 1981). This would represent a maximum dry-matter intake of over 16 kg/day for a 500-kg elk, almost 10 kg/day for a 300-kg elk, and 3.3 kg/day for a 100-kg elk. At these rates of intake, elk could theoretically ingest enough feed to meet maintenance nitrogen requirements, even with forages containing only 4% crude protein (Fig. 8). However, such high intakes are not likely with low-protein feeds because they are usually associated with high fiber contents (Urness et al. 1975), resulting in slower rumen passage rate (Ewing 1917, Mautz and Petrides 1971), which in turn exerts a physical limit upon feed intake (Campling and Balch 1961). Additionally, forages that contain low levels of protein generally have low apparent energy digestibilities (Phillips and Laughlin 1949), high lignin content (Schommer 1978), and often significant levels of tannins (Feeny 1970, Prins and Geelen 1968), all of which decrease voluntary dry-matter intake (Blaxter et al. 1966, McLeod 1974). Given that animals tend to consume feeds to meet energy needs (Balch and Campling 1962, Montgomery and Baumgardt 1965, Holter et al. 1979*a*), nitrogen requirements for maintenance during spring, summer, and fall can be met incidentally because

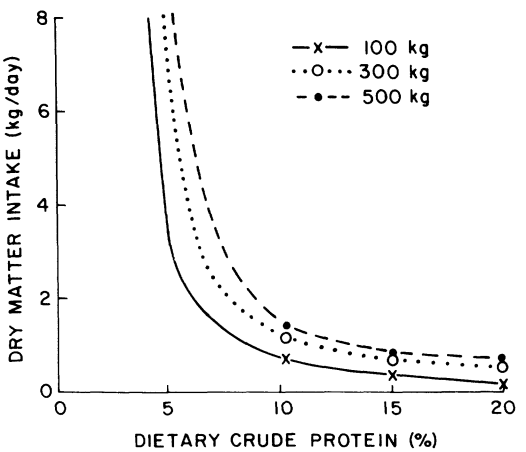

Fig. 8. Predicted dry-matter intakes needed by 100-, 300-, and 500-kg elk to meet maintenance nitrogen requirements at various crude-protein contents.

crude protein concentrations of forages then are generally >10% (Schommer 1978). However, during winter when crude-protein content of available forages falls below 5% and quantities of forages are limited (Nelson and Leege 1980, Schommer 1978), digestible nitrogen intake may then become critical, as it is more likely to drop below the maintenance requirement.

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