Dry Matter, Nitrogen, and Energy Digestibility in the North American Porcupine (*Erethizon dorsatum*)

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Introduction

Herbivores are often challenged in meeting dietary requirements because many forages contain low levels of nutrients, high concentrations of plant fiber, and plant secondary compounds which decrease the quality of a diet. Tree bark, for example, contains few vitamins, minerals, carbohydrates, fats and proteins, but does contain high amounts of fiber, such as lignin and cellulose, which decrease the digestibility of plant matter and its retention time in non-ruminants. A decrease in retention time corresponds with a decreased opportunity to extract nutrients from the forage. Although foliage contains relatively high amounts of nutrients, many of these forages also contain chemical compounds that may reduce an animal's ability to digest food. For example, tannins, water-soluble phenolic compounds, inhibit protein digestibility in many animals (Koenig, 1991). Thus, many herbivores may experience physiologic difficulties extracting from forages energy, protein and other nutrients necessary to fuel metabolic processes and build and maintain body tissue.

Diet quality for an animal must not be measured only by the constituents of the diet, but also by the animal's nutritional requirements, and digestive and behavioral adaptations (Hume et al., 1993). The North American porcupine (*Erethizon dorsatum*), a relatively small opportunistic herbivore and a non-coprophagic hindgut fermenter that subsists on forages such as cambium and tannin-containing vegetation, overcomes the difficulties associated with a herbivorous diet. Little, however, is understood about the porcupine's physiologic adaptations and nutritional requirements. Fournier and Thomas (1997) studied the protein and energy requirements of the porcupine using a pelleted diet and suggested porcupines have physiologically adapted to low protein diets by reducing protein loss in the feces, thereby increasing protein retention. They also suggested porcupines lack the ability to detect a nitrogen deficiency and adjust their nitrogen and energy intake accordingly. In this study we assessed the nutritive quality of several natural forages, that will test the range of tolerances and capabilities of the porcupine's digestive tract. Our objectives were:

1. To determine the dry matter (DM), energy, and protein digestibilities of each forage in porcupines.

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2. To determine how fiber and tannins affect protein and energy digestibilities in porcupines.
3. To determine the minimum protein and energy intake requirements for porcupines fed a natural diet.

Methods

This study took place at Washington State University (WSU) from July 1997 to July 1998. During a series of feeding trials we presented 4 to 5 porcupines with each of the following natural diets: Pacific willow leaves (*Salix lasiandra*), apples (Macintosh variety), red oak acorns (*Quercus rubra*), and English oak acorns (*Quercus robur*) (Table 1). We conducted 5-day total collection trials following a 5-day diet transition period, characterized by a gradual transfer from a pelleted diet to the trial diet, and a 3- to 5-day pretrial, during which animals were moved from their outside facilities to indoor metabolic crates and given time to equilibrate to both the diet and their temporary housing. Mineral blocks were provided for each animal, and food and water were offered ad libitum. Food was weighed and fed to the porcupines each morning of the trial. Orts were collected, weighed and subtracted from the amount given the previous day to determine how much food each animal ingested. Animals were weighed before and after each 5-day collection period.

Feces fell to mesh screens placed below the cages and urine was funneled to bottles containing approximately 5 ml of HCl acid. Each day we collected samples of food, feces, and urine and stored them at –20°C for later analysis. We dried samples of food, feces and orts daily at 100°C for 24 hr to determine the dry matter content. At the end of a trial, each individual's food, feces, and urine were pooled across the 5-day trial. Food and feces were dried at approximately 50°C for 4 days, ground and stored for later analysis.

We measured the gross energy of food, feces and urine using bomb calorimetry. Nitrogen content of samples was determined by the Kjeldahl procedure. Neutral detergent fiber (NDF) of food samples was extracted as in Goering and Van Soest (1970). Tannin binding capacity of forages was determined by the bovine serum albumin (BSA) (Robbins et al., 1987).

Apparent and true digestibilities of dry matter, nitrogen and energy were calculated as in Robbins (1993). To determine minimum nitrogen requirements we conducted a linear regression of nitrogen balance against dietary nitrogen intake. Metabolic fecal nitrogen was estimated to be the y-intercept of the regression between dietary nitrogen and digestible nitrogen (g N/100 g food). The y-intercept of the regression between dietary nitrogen intake and urinary nitrogen provides an estimate of endogenous urinary nitrogen. We compared digestion and passage among diets with ANOVA and Duncan's mean separation technique

Results

Animals maintained constant mass on all trials except for the willow trial. Dry matter intake varied over the trials ($F = 5.49$, $P = 0.0117$; Table 2) ranging from a mean ± standard error of 73.9 g/day

± 7.0 g/day on the red oak acorn trial to 233.7 g/day ± 39.1 g/day on the apple trial. Apparent dry matter digestibility of apples and English oak acorns were significantly higher than that of willow and red oak acorns ($F = 60.67$, $P < 0.0001$; Table 2). Gross energy intake ($F = 4.61$, $P = 0.0208$), apparent digestible energy ($F = 65.57$, $P < 0.0001$), and digestible energy intake ($F = 8.94$, $P = 0.0018$) were higher for the apple and English acorn diets than the willow and red oak acorn diets.

Nitrogen balance was not significantly related to total nitrogen intake. Aside from two animals during the apple trial, all porcupines experienced negative nitrogen balance during the trials. Nitrogen balance occurred at a nitrogen intake of 244 mg N/kg$^{0.75}$/day (Figure 1). Urinary nitrogen was significantly related to nitrogen intake ($r^2 = 0.72$, $P < 0.0001$; Figure 2). Endogenous urinary nitrogen was 46.7 mg/kg$^{0.75}$/day.

When combining the apple trial (our only tannin-free diet) with the pelleted diets of Fournier and Thomas (1997) digestible nitrogen was significantly correlated with dietary nitrogen ($r^2 = 0.98$, $P = 0.006$; Figure 3). Metabolic fecal nitrogen was 0.3 g N/kg dry matter intake, and true nitrogen digestibility was 94%.

Discussion

Dry matter digestibility for the apple, English oak acorn, and red oak acorn diets by porcupines ranged from 77.6 to 96.4%. These numbers are similar to the dry matter digestibilities found by Fournier and Thomas (1997) which ranged from 81 to 98%. Dry matter digestibility for the willow diet, however, was considerably lower ranging from 55 to 66%. Among rodents dry matter digestibilities as low as 54 to 60% are not uncommon (Batzli and Cole, 1979; Karasov, 1982; Farrell and Christian, 1987). The high fiber content of willow compared with the other diets is the probable cause of lower digestibility.

Porcupines achieved nitrogen balance at 244 mg/kg$^{0.75}$/day in our trials. This is somewhat lower than that found by Fournier and Thomas (1997) who reported porcupines reached nitrogen balance at 389 mg/kg$^{0.75}$/day and only half that of the mean nitrogen balance for eutherians (582 ± 235 mg/kg$^{0.75}$/day) (Robbins 1993). Because porcupines eat low nitrogen diets, the ability to achieve nitrogen balance at low levels of nitrogen intake is beneficial.

To reach nitrogen equilibrium an animal must ingest enough nitrogen to counteract the minimum constant loss of nitrogen in the feces and urine. Metabolic fecal nitrogen (MFN) and endogenous urinary nitrogen measure the minimum constant loss of nitrogen in the feces and urine (Robbins, 1993). We established metabolic fecal nitrogen for porcupines to be approximately 0.3 g N/kg dry matter intake, which coincides with Fournier and Thomas's (1997) estimate of 0.4 g N/kg dry matter intake. We, however, determined endogenous urinary nitrogen (46.7 mg/kg$^{0.75}$/day) to be much lower than did Fournier and Thomas (223.1 mg/kg$^{0.75}$/day; 1997) as well as the non-ruminant eutherian mean (160 ± 22 mg/kg$^{0.75}$/day; Robbins, 1993). Our findings of lower endogenous urinary nitrogen correspond with the lower nitrogen balance of our porcupines.

Preliminary results from our study using natural forages support the findings of Fournier and Thomas (1997). We are currently conducting more feeding trials and waiting for the results from our tannin analysis.

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Table 1. Dry composition of forages fed to captive porcupines.

Constituents	Willow	Apple	English oak acorn	Red oak acorn
NDF (%)	46.37	15.51	13.07	17.46
Energy content (kJ/g)	18.59	16.53	21.93	21.22
Nitrogen (%)	2.7	0.41	0.57	1.09
Crude Protein (%)	16.86	2.55	3.54	6.83

Table 2. Mean and standard error for dry matter, energy, and nitrogen intake and digestibility for North American porcupines. Different letters within a column signify significant differences among means (alpha = 0.05).

Diet	Willow	Apple	English oak acorn	Red oak acorn
Dry matter intake (g/day)	97.16 ± 36.26[bc]	233.69 ± 39.06[a]	172.55 ± 26.08[ab]	73.97 ± 6.99[c]
Dry matter digestibility (% DM)	61.69 ± 2.34[c]	95.62 ± 0.40[a]	90.96 ± 1.10[a]	83.55 ± 2.97[b]
Gross energy intake (kJ/day)	1805.71 ± 729.74[b]	3863.91 ± 645.90[a]	3784.87 ± 572.16[a]	1569.87 ± 148.32[b]
Apparent energy digestibility (% DM)	54.93 ± 2.72[c]	94.00 ± 0.61[a]	91.90 ± 0.91[a]	83.91 ± 3.60[b]
Digestible energy intake (kJ/day)	938.97 ± 322.89[b]	3641.14 ± 629.59[a]	3495.17 ± 551.48[a]	1314.79 ± 134.48[b]
Nitrogen intake (g/day)	2.62 ± 1.06[a]	0.95 ± 0.15[b]	0.98 ± 0.15[b]	0.81 ± 0.08[b]
Apparent nitrogen digestibility (% DM)	51.5 ± 3.46[a]	36.58 ± 6.24[ab]	4.73 ± 10.01[b]	29.33 ± 16.44[ab]

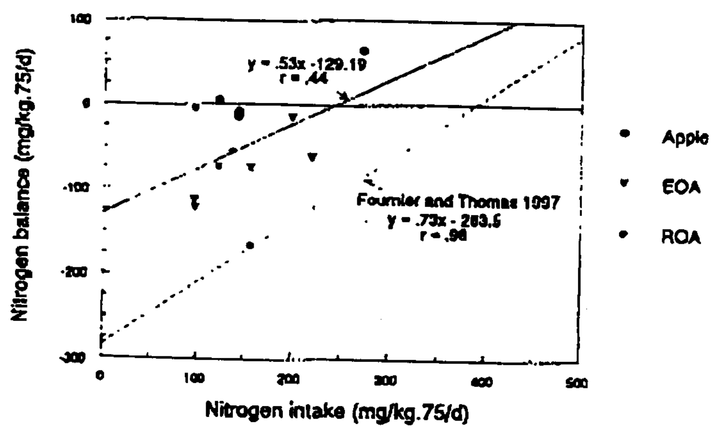


Figure 1. Relationship between nitrogen balance and total nitrogen intake of the North American porcupine.

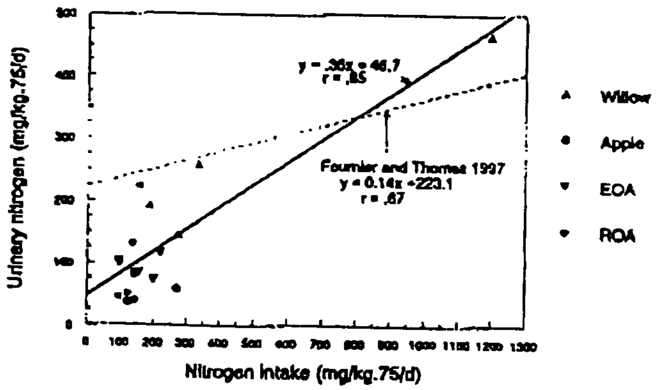


Figure 2. Relationship between urinary nitrogen and total nitrogen intake of the North American porcupine.

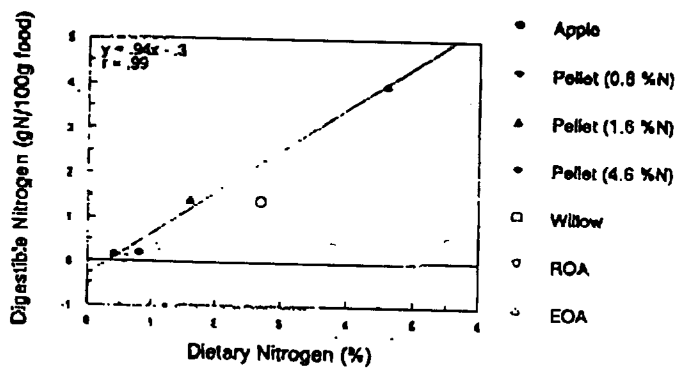
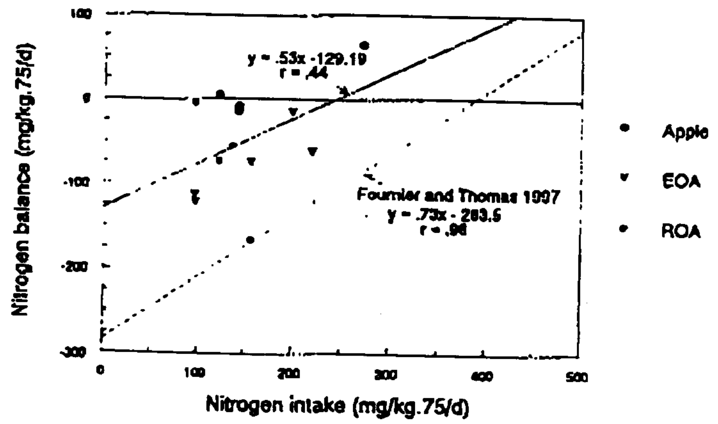


Figure 3. Relationship between digestible nitrogen and nitrogen content of apples and pellets (Fournier and Thomas 1997) consumed by North American porcupines. Willow, red oak acorn (ROA) and English oak acorn (EOA) diets are not included in the regression because of tannins.



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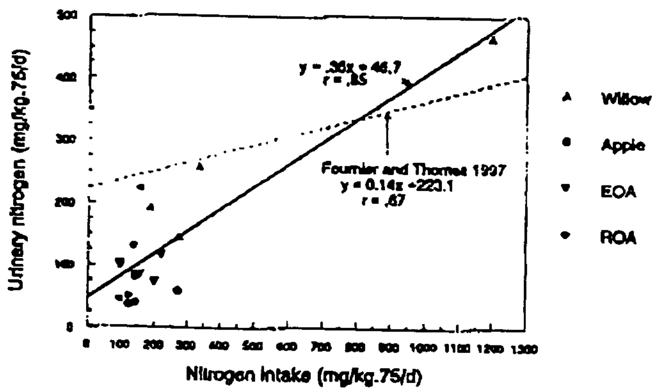
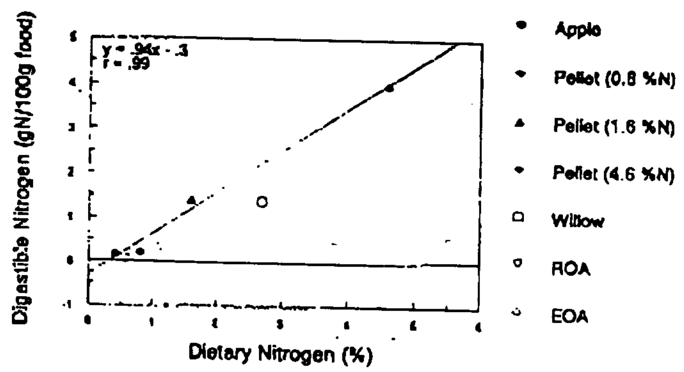


Figure 2. Relationship between urinary nitrogen and total nitrogen intake of the North American porcupine.



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