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DIGESTIBILITY AND ASSIMILATION OF NATURAL FORAGES BY MUSKRAT

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Abstract: Knowledge of the forage intake and digestive efficiencies of muskrat (*Ondatra zibethicus*) is essential for developing an understanding of their habitat requirements and their impact on emergent vegetation. We performed 30 complete digestibility, energy-, and nitrogen-balance trials on 6 adult male muskrat fed 5 diets: (1) sedge (*Carex atherodes*) shoot, (2) softstem bulrush (*Scirpus validus*) shoot, (3) hybrid cattail (*Typha* × *glauca*) shoot, (4) cattail rhizome, and (5) a combination of cattail shoot and rhizome. Dry matter (DM) digestibilities ranged from 61.2 to 70.6%. Neutral detergent fiber (NDF) digestibilities varied from 40.0 to 59.6% for these emergent plant diets with NDF levels ranging from 44.6 to 62.1%. Microbial fermentation of fiber accounted for 39.4% of digestible energy (DE) intake. Muskrat can digest fiber as well as can many ruminants and pseudoruminants, but can do so more efficiently than other rodents. Apparent digestibility of dietary crude protein (DCP) was highest ($P < 0.001$) for sedge (73.6%) and lowest ($P = 0.001$) for the cattail rhizome diet (7.2%). However, the daily nitrogen intake (DNI) required by muskrat to maintain tissue balance on a cattail rhizome diet (0.599 g $N/kg^{0.75}$/day) was less than half the daily intake required for all other diets combined (1.266 g $N/kg^{0.75}$/day) ($P < 0.001$). This implies the existence of a protein conservation mechanism by which muskrat could negate the effects of low dietary crude protein during winter.

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Key words: aquatic plants, digestibility, energy, fiber, Manitoba, muskrat, nitrogen, nutrition, *Ondatra zibethicus*, wetlands.

A goal in wetland management is to maintain marshes at, or near, their maximum potential for perpetuating wildlife resources. Achieving this objective requires an understanding of the muskrat's role in modifying marsh ecosystems because this rodent is often the prominent vertebrate consumer of marsh vegetation (Krummes 1940, McCabe 1982). Muskrat are versatile feeders, capable of exploiting diverse food sources (Errington 1941; Bellrose 1950; Danell 1977, 1978), yet little is known regarding their energy and nutritional requirements (Westworth 1974, Welch 1980, Jelinski 1989). Estimates of the rate of food intake, energy assimilation, and coefficients of digestibility are essential to developing an understanding of muskrat nutritional needs.

Such information should help managers assess the relative nutrient value of different forages and the potential role of these animals in providing biological control of aquatic emergents (Danell 1979, McCabe 1982). Our understanding of habitat selection and population dynamics of muskrat in wetland ecosystems also would be enhanced (Messier et al. 1990, Clark and Kroeker 1993).

Our objective was to evaluate digestibilities of 5 common emergent plant forages consumed by muskrat in northern prairie marshes. We also estimated the minimum energy required for maintenance on each diet, as well as the efficiency with which muskrat convert dietary protein into body tissue.

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METHODS

We livetrapped 6 adult male muskrat at Oak Hammock Marsh, Manitoba (50°06′N, 97°07′W), in early May 1990. We transported animals to the University of Manitoba, where they were held in controlled environment chambers maintained at 14 ± 1 C with a 12 hour light : 12 hour dark photoperiod (MacArthur 1979). Relative humidity was kept at 77–94% for the study duration. Except during digestion trials, we maintained animals on a diet of Wayne Lab-Blox rodent chow supplemented with apples and carrots. All animals were acclimated to the holding facilities for ≥3 weeks before we began digestion trials. We derived in vivo digestion estimates, using the total balance trial method in which all feed ingested and wastes produced were weighed and subsequently analyzed (Robbins 1993).

During digestion trials, we housed animals individually in digestion cages (106 × 52 × 46 cm), each furnished with a fiber glass nest box (27 × 23 × 25 cm). We suspended each cage over a hardware cloth screen (0.3-cm mesh) for fecal collection; a plastic drape beneath the screen caught and directed all urine into a collection vial containing 0.7 mL concentrated HCl. We provided drinking water ad libitum.

We performed 30 digestion trials between 23 May and 14 September 1990. Each trial consisted of a 5-day pretrial session when muskrat adjusted to the test ration and digestion cage, followed by a 5-day fecal and urine collection period. Successive trials with different diets were punctuated by rest periods, each ≥5 days, when muskrat were fed the standard laboratory diet described above.

We tested 5 emergent plant diets: (1) sedge shoot, (2) softstem bulrush shoot, (3) hybrid cattail shoot, (4) cattail rhizome, and (5) a mixed cattail diet consisting of 67% shoot and 33% rhizome. We selected the mixed diet to test for possible associative digestion effects (Robbins 1993), and the predominance of shoots in this diet was based on analyses of early summer feeding platforms used by muskrat. We collected forage rations at Delta Marsh, Manitoba (50°11′N, 98°23′W), and stored them at 5 C to reduce plant respiration and deterioration. We harvested vegetation on the day before each pretrial and trial session. Only the lower 25–40 cm of each plant was presented to animals. This preparatory step was based on space restrictions in the digestion cage and on the natural preference of muskrat for basal portions of emergent plants (Westworth 1974, Danell 1977, Welch 1980).

During digestion trials completed between 19 June and 31 August, we randomly assigned muskrat the cattail shoot, mixed cattail, and bulrush shoot diets. We tested all animals on the sedge diet between 23 May and 15 June, and on the cattail rhizome diet between 22 August and 14 September. We tested the sedge diet first because other emergents were unavailable in the spring and sedge often constitutes the principal forage consumed by muskrat during this season (Takos 1947, Sather 1958, Danell 1978). We tested the cattail rhizome diet last because roots and rhizomes of aquatic plants constitute a major portion of the autumn and winter diet of muskrat (Takos 1947, Bellrose 1950, Jelinski 1989). We assigned each muskrat a given diet only once, thus providing 6 digestibility estimates for each of the 5 diets tested.

In each trial, we fed preweighed (ad libitum) rations to muskrat 3 times daily. A sample of each test ration was also weighed and left on a

Table 1. Chemical composition of 5 emergent plant diets fed to muskrats during 10-day digestibility trials, conducted in southern Manitoba, 1990.

Item	Sedge shoot		Softstem bulrush shoot		Cattail shoot		Cattail rhizome		Cattail shoot and rhizome	
	$\bar{x}$[a]	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Ash (%)	10.0C[b]	0.0	12.6B	1.1	12.6B	0.6	17.0A	0.5	14.2B	0.6
Dry matter content (%)	13.2A	0.5	10.1B	0.7	8.7C	0.4	9.5BC	0.3	8.2C	0.0
Gross energy (kJ/g)	17.0A	0.0	16.3B	0.2	16.0BC	0.1	15.1D	0.2	15.5CD	0.1
Ash-free energy (kJ/g)	18.9A	0.0	18.7AB	0.1	18.3BC	0.1	18.2BC	0.4	18.1C	0.1
Crude protein (%)	16.8A	0.4	6.7B	0.5	6.0BC	0.3	5.5C	0.1	5.9BC	0.3
Neutral detergent soluble (%)	41.6BC	0.3	37.9C	1.8	42.0BC	1.3	55.4A	2.7	45.4B	1.7
Neutral detergent fiber (%)	58.4BC	0.3	62.1C	1.8	58.0BC	1.3	44.6A	2.7	54.6B	1.7
Acid detergent fiber (%)	31.3C	0.0	38.6A	0.9	35.9B	0.6	25.9D	0.3	31.5C	1.8

[a] $n = 6$ samples for all diets.
[b] Within each row, means sharing same letter are not different ($P > 0.05$).

tray outside the digestion cage. During each daily collection period, we weighed the ration sample and all feces and uneaten rations (orts) to the nearest 0.01 g, then froze them at −20 C for subsequent analyses. We recorded mass and total volume of urine produced daily and pooled urine samples for each animal for the 5-day trial. We weighed muskrat daily to determine mass changes during pretrial and trial periods.

We dried ration samples, orts, and feces to constant mass (48–72 hr) at 70 C and then ground them through a 1-mm-mesh screen in a Wiley mill. We sent a portion of each ground sample to a feed analysis laboratory (Dep. Anim. Sci., Univ. Manitoba, Winnipeg) for protein (Kjeldahl N × 6.25), acid detergent fiber (ADF), and NDF determinations (Goering and Van Soest 1970, Assoc. Off. Anal. Chem. 1984). We calculated neutral detergent solubles (NDS) as 100% − NDF. We analyzed urine samples for nitrogen and energy content. Gross energy content of food, feces, and urine was obtained by duplicate measurements in an adiabatic oxygen bomb calorimeter (Parr 1241 Calorimeter, Parr Instrum. Co., Moline, Ill.). We first lyophilized urine samples and then mixed them with a known mass of mineral oil to ensure complete combustion. We determined total ash content by combustion of 2-g samples for 2 hours at 600 C. We calculated the proportion of energy obtained from consumed fiber (ration NDF − orts NDF) following Hammond and Wunder (1991). We evaluated animal and diet effects using 2-way analysis of variance and compared mean values with t-tests for pairwise comparison of least-squares means (PROC GLM, SAS Inst. Inc. 1990:891).

RESULTS

Ration Analyses

The gross energy content of the 5 emergent plant diets fed to muskrat varied inversely with ash content (Table 1). On an ash-free basis, the energy content of these diets varied over a narrow range, from 18.1 to 18.9 kJ/g. The protein content of sedge was 2.5–3.0 times higher than that of the other diets (Table 1). Fiber content generally was highest for bulrush and lowest for the cattail rhizome diet (Table 1). Dry matter content was low in all 5 emergent diets (8.2–13.2%).

Because not all diets were tested concurrently, some observed differences may reflect changes in plant phenology. However, results for bulrush, mixed cattail, and cattail shoots were from samples collected over 2 months and ranged from newly emerged to mature shoots. Variance for these samples is small and generally consistent with that of diets tested first (sedge) and last (cattail rhizomes) (Table 1).

Intake and Digestibility of Nutrients

Analysis of variance of pooled data for all 5 diets revealed no differences ($P > 0.05$) among animals in any of the variables tested. In all cases, daily DM and gross energy intake were highest on cattail rhizomes, but similar for the remaining diets (Table 2). Digestibility coefficients for DM, DE, and metabolizable energy (ME) also tended to be highest for the cattail rhizome diet (Table 3). Apparent DCP digestibility was highest (73.6%; $P < 0.001$) for the sedge and lowest (7.2%; $P = 0.001$) for the cattail rhizome diet (Table 3).

Table 2. Dry matter, gross energy (GE), digestible energy (DE), and metabolizable energy (ME) intake of 6 adult male muskrat fed 5 emergent plant diets, in southern Manitoba, 1990.

Item	Sedge shoot		Softstem bulrush shoot		Cattail shoot		Cattail rhizome		Cattail shoot and rhizome	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
$\bar{x}$ body mass (g)	901.4B[a]	44.0	889.7B	40.6	896.0B	56.1	964.5A	52.4	912.0B	49.4
Dry matter intake (g)	32.5B	1.3	35.0B	2.4	28.6B	3.4	47.3A	5.3	31.2B	3.9
Dry matter intake ($g/kg^{0.75}/day$)	35.4B	1.8	38.5B	2.7	31.4B	3.9	48.7A	5.0	33.3B	3.4
GE intake/BM[b] ($kJ/kg^{0.75}/day$)	602.7B	29.7	618.3B	45.6	483.8B	66.4	776.4A	73.6	521.0B	56.3
DE intake/BM ($kJ/kg^{0.75}/day$)	367.6B	21.9	375.5B	22.9	288.4B	49.4	534.8A	65.3	296.0B	36.8
ME intake/BM ($kJ/kg^{0.75}/day$)	327.5B	20.9	354.0B	23.2	264.5B	47.6	521.4A	64.6	277.3B	36.6

[a] Within each row, means sharing same letter are not different ($P > 0.05$).
[b] BM = body mass $kg^{0.75}$.

Fiber digestibility varied little among diets. Though not significant ($P = 0.090$–0.523), NDF and ADF digestibilities tended to be lowest on cattail rhizome and highest on bulrush and sedge diets (Table 3). Dry matter digestibility varied inversely with dietary NDF (DM digestibility = 89.14 − 0.44 NDF, $r^2 = 0.26$, $n = 30$, $P = 0.004$), but showed no relationship with forage ADF content. Digestibilities of NDF and ADF varied with percentages of these constituents in the diet: NDF digestibility = −6.47 + 1.06 NDF ($r^2 = 0.39$, $n = 30$, $P < 0.001$); ADF digestibility = 22.38 + 0.92 ADF ($r^2 = 0.14$, $n = 30$, $P = 0.042$). Digestibility of the NDS fraction was highest for muskrats fed the cattail rhizome diet ($P = 0.043$). Apparent digestible NDS correlated with the NDS content of the diet ($r^2 = 0.99$, $n = 30$, $P < 0.001$). The regression equation relating these variables (NDS digestibility = 17.979 + 0.923 NDS) yielded a true NDS digestibility of 92.3%.

Partitioning of Dietary Nitrogen

For all diets except sedge, the mean DNI of muskrats was similar (Table 4). The DNI of muskrat fed sedge was >2 times that recorded for any other diet ($P < 0.001$). The regression of apparent digestible nitrogen (ADN) on DNI yielded the equation ADN ($g\ N/kg^{0.75}/day$) = −0.293 + 0.965 DNI ($r^2 = 0.92$, $n = 30$, $P < 0.001$). This equation provides a true nitrogen digestibility (TND) estimate of 96.5%. Calculated TND estimates for individual diets were 98.2% for sedge, 95.1% for bulrush, 98.5% for cattail shoot, 99.5% for cattail rhizome, and 88.4% for mixed cattail.

Mean fecal nitrogen loss varied little with diet. However, mean urinary nitrogen loss was variable (Table 4; $P < 0.001$). Endogenous urinary nitrogen loss was only 0.041 $g\ N/kg^{0.75}/day$, following the regression total urinary nitrogen excreted ($g\ N/kg^{0.75}/day$) = 0.041 + 0.710 DNI

Table 3. Apparent digestibility (%) of nutrients in 5 emergent plant diets fed to 6 adult male muskrat, in southern Manitoba, 1990.

Item	Sedge shoot		Softstem bulrush shoot		Cattail shoot		Cattail rhizome		Cattail shoot and rhizome	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Dry matter	64.0B[a]	1.5	65.9AB	1.2	62.7B	2.0	70.6A	3.4	61.2B	2.8
Digestible energy	60.9B	1.5	61.1AB	1.1	57.7B	3.4	68.3A	3.3	56.9B	2.8
Metabolizable energy	54.2B	1.6	57.5B	1.0	52.3B	3.9	66.5A	3.3	53.1B	3.0
Dietary crude protein	73.6A	1.2	33.4C	4.6	47.1B	2.1	7.2D	6.6	27.5C	6.0
Neutral detergent solubles	68.5B	1.0	72.9B	0.9	69.2B	2.3	79.6A	3.7	69.3B	2.0
Neutral detergent fiber	59.6A	2.7	59.4A	1.6	53.5A	3.4	40.0B	7.6	50.0AB	4.1
Acid detergent fiber	55.5AB	3.3	63.1A	1.5	52.0B	3.9	44.7B	7.7	47.1B	3.4

[a] Within each row, means sharing same letter are not different ($P > 0.05$).

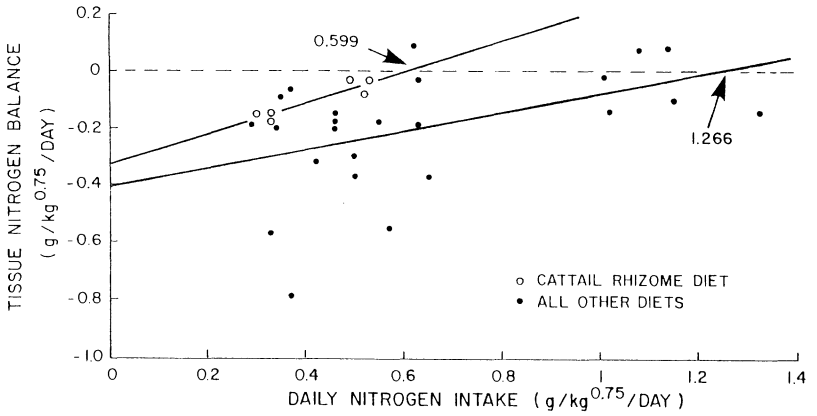

Fig. 1. The relationship between tissue nitrogen balance (TNB) and daily nitrogen intake (DNI) of 6 adult male muskrat fed aquatic emergent plant diets during summer and early autumn, Manitoba, 1990. The 5 rations tested were sedge shoot, softstem bulrush shoot, cattail shoot, cattail rhizome, and a mixture of cattail shoot and rhizome. Regression lines were fitted by the method of least-squares (cattail rhizome diet, TNB = −0.334 + 0.557 DNI, $n = 6$, $r^2 = 0.83$, $P = 0.012$; other diets combined, TNB = −0.410 + 0.324 DNI, $n = 24$, $r^2 = 0.22$, $P = 0.022$).

($r^2 = 0.52$, $n = 30$, $P < 0.001$). On all diets, urinary energy loss was correlated with urinary nitrogen ($r^2 = 0.65$, $n = 30$, $P < 0.001$) and ration nitrogen levels ($r^2 = 0.63$, $n = 30$, $P < 0.001$).

Regressing tissue nitrogen balance on DNI for all diets except cattail rhizome revealed that muskrat must consume 1.266 g N/kg$^{0.75}$/day to maintain nitrogen balance (Fig. 1). Following Holter et al. (1979), the level of dietary crude protein needed to meet this daily nitrogen requirement was 22.8% at a mean forage intake of 34.65 g/kg$^{0.75}$/day. However, the maintenance nitrogen requirements of muskrat fed the cattail rhizome diet was only 0.599 g N/kg$^{0.75}$/day. This is less than half the DNI required by muskrat on other diets (Fig. 1) and could be met with a crude protein level in cattail rhizomes of only 7.69%.

DISCUSSION

Digestibility of Nutrients

Muskrat densities in marshes vary with the types of emergent vegetation present (Boutin and Birkenholz 1987, Messier et al. 1990). Clark and Kroeker (1993) found that vegetational succession can influence recruitment and survival of muskrat in prairie marshes. However, the extent to which demographic factors and habitat selection are influenced by diet remains unknown (Lacki et al. 1990). Although forage quality and palatability have been implicated as possible factors influencing diet choice of muskrat (Errington 1941, Takos 1947, Bellrose 1950), we found little variation in digestive efficiencies. Muskrat appeared to digest sedge, bulrush, and cattail shoots to similar extents during summer, implying that other variables such as forage availability, predation, water level, or suitability for lodge construction may have a greater bearing on selection of habitat.

Although no associative digestion effect was observed on the mixed cattail diet, all 6 muskrat showed a preference for the rhizome component of this ration. The diet consisted of 67% shoot and 33% rhizome, yet the rhizome fraction constituted 52% of DM intake. Muskrat preference for the rhizome fraction was also demonstrated in laboratory feeding trials performed by Akkermann (1975), and likely reflects the superior nutritional value of this portion of the plant.

The DM digestibilities reported herein are 20–25% higher than estimates derived for other rodent species fed diets of similar fiber content. Results reported by Batzli and Cole (1979) suggest that brown lemmings (*Lemmus sibiricus*) digest sedge (*C. aquatilis*) only about half as well as the muskrat maintained in this study on a similar sedge (*C. atherodes*) diet. The DM and gross energy digestibilities of lemmings fed *C. aquatilis* were only 33.2 and 34.0%, respectively, compared with 64.0 and 60.9% for muskrat maintained on *C. atherodes*.

Several studies have indicated that small herbivores can use plant NDF as a major source of dietary energy. The NDF fraction accounted for 19–32% of DE in rodents fed diets containing 39–49% NDF (Hammond and Wunder 1991, Justice and Smith 1992, Nagy and Negus 1993).

Table 4. Daily intake and partitioning of dietary nitrogen in 6 captive muskrat fed 5 emergent plant diets, in southern Manitoba, 1990.

Item (g/kg$^{0.75}$/day)	Sedge shoot		Softstem bulrush shoot		Cattail shoot		Cattail rhizome		Cattail shoot and rhizome	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Nitrogen intake	1.12A[a]	0.05	0.51B	0.06	0.47B	0.03	0.42B	0.04	0.44B	0.05
Fecal nitrogen loss	0.30BC	0.02	0.34AB	0.04	0.25C	0.02	0.38A	0.02	0.32ABC	0.04
Urinary nitrogen loss	0.87A	0.06	0.51B	0.10	0.47BC	0.07	0.15D	0.02	0.31CD	0.05
Tissue nitrogen balance	−0.04A	0.04	−0.33C	0.13	−0.25BC	0.07	−0.10AB	0.03	−0.19ABC	0.05
Apparent digestible nitrogen	0.83A	0.04	0.18BC	0.03	0.22B	0.01	0.04D	0.03	0.12C	0.03

[a] Within each row, means sharing same letter are not different ($P > 0.05$).

By comparison, muskrat obtained an average of 39.4% of their DE intake from the microbial fermentation of fiber ($\bar{x}$ NDF consumed = 43.1%). Whereas meadow voles (*Microtus pennsylvanicus*) experience high mortality when dietary NDF exceeds 55% (Keys and Van Soest 1970), muskrat maintained mass and appeared healthy on diets containing ≤67% NDF. The muskrat capacity to digest plant fiber exceeds that of other small rodents and may rival digestion capabilities of several ruminants and pseudoruminants. Muskrat apparently can digest fiber with an efficiency comparable with that of collared peccaries (*Tayassu tajacu*) (Carl and Brown 1986), mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) (Baker and Hansen 1985). These similarities do not likely arise from variability in plant digestion inhibitors because the lignin content of cattail shoots (3.4%; Lacki et al. 1990) is close to that (4.7–5.4%) of diets tested in the latter studies.

Forage quality and gut morphology of mammals are strongly interdependent. Increased dietary fiber, for example, often stimulates caecal growth, thereby lengthening digesta retention time and facilitating digestion of cell wall constituents (Gross et al. 1985, Hammond and Wunder 1991, Loeb et al. 1991). Therefore, the muskrat's ability to handle large quantities of dietary fiber may reflect the species' large, well-developed caecum (Virgl and Messier 1992), allowing for a high fermentation capacity and large absorptive surface area.

Like the muskrat, nutria (*Myocastor coypus*) also feed predominantly on basal shoots and rhizomes of aquatic plants, including cattail and bulrush. Nutrias reportedly have a long digesta retention time (45 hr) and high NDF digestibility (48%) on a diet composed of 32.5% NDF (Sakaguchi and Nabata 1992). As Sakaguchi and Nabata (1992) noted, these traits could reflect the occurrence of coprophagy in this South American rodent. Coprophagy was not prevented in our experiments and may have contributed to the high fiber digestibilities we observed. The high thermoregulatory costs of aquatic foraging, especially in winter, also may select for large gut capacity and high fiber digestibility in the muskrat.

Partitioning of Dietary Nitrogen

Our estimate of TND in the muskrat (96.5%) is close to values (94.0–98.5%) reported for other similar-sized caecal fermentators (Nagy et al.

1976, Carl and Brown 1985, Meyer and Karasov 1989). High TND and relatively low true NDS digestibility (92.3%) observed in muskrat may, to some extent, reflect the presence of secondary plant compounds in the emergent diets (Robbins 1993).

Extrapolating the regression of ADN on DNI to zero nitrogen intake yielded a metabolic fecal nitrogen loss of 0.293 g N/kg$^{0.75}$/day, or 0.78 g N/100 g DM intake. The latter estimate is near the upper limit of the range reported for caecal digestors (0.3–0.9 g N/100 g DM intake). This is to be expected because high-fiber forages tend to yield large metabolic nitrogen losses in feces (Robbins 1993).

Muskrat voided 93–198 mL urine/day, a trend likely reflecting the high water content of ingested forage. However, the estimated endogenous urinary nitrogen loss of 0.04 g N/kg$^{0.75}$/day is lower than in other nonruminant eutherians studied (range 0.13–0.18 g N/kg$^{0.75}$/day; Robbins 1993).

The finding that muskrat tended to be in a slightly negative nitrogen balance on all 5 emergent plant diets (Table 4) suggests that animals consuming these diets alone would be unable to maintain body protein over extended periods. This observation, together with the high dietary crude protein requirement (22.8%) of muskrat fed emergent vegetation, suggests the need for a supplemental source of nitrogen in the summer diet. Such a need could explain the consumption of animal matter in at least some muskrat populations (Errington 1941, Stearns and Goodwin 1941). Although muskrats may feed opportunistically on clams, mussels, snails, and carrion throughout the year, their consumption of animal matter often appears highest in summer (Triplet 1983, Convey et al. 1989, Neves and Odom 1989), when dietary nitrogen requirements presumably are greatest.

Our estimate of the minimum level of dietary protein (7.69%) required for muskrat to maintain tissue nitrogen balance on cattail rhizomes is close to winter protein levels previously reported for this plant component (7.61–7.75%; Freudethal 1922, Stearns and Goodwin 1941). This estimate is lower than the 15% crude protein that is generally recognized as a minimal requirement in rodent diets (Jelinski 1989). How muskrat reduce their nitrogen requirements on cattail rhizomes, the dominant forage consumed by these rodents during fall and winter, is unknown. Urea recycling, coprophagy, urine drinking, and selective foraging are all potential physiological and behavioral tactics by which mammals can negate the effects of low dietary protein (Smith et al. 1975, Robbins 1993). Clearly, more research on this aspect of muskrat nutrition is required, especially as it relates to muskrat winter ecology.

Maintenance Energy and Forage Requirements

The energy required for maintenance can be estimated if daily food consumption and assimilation efficiencies are known and if the mass and proximate composition of the animal remains constant (Robbins 1993). Change in body mass during digestion trials varied only from −3.2 to 3.6% ($\bar{x}$ = −1.3%). This, together with the absence of any obvious relationship between tissue nitrogen balance and DE intake ($r^2 = 0.01$, $n = 30$, $P = 0.595$), suggests that our animals obtained adequate energy from their diet and that tissue catabolism was minimal (Mould and Robbins 1981). Our estimates of minimal DE and ME intake in summer, derived for all diets except cattail rhizome, were 332 and 306 kJ/kg$^{0.75}$/day, respectively. These values are close to the estimate (379 kJ/kg$^{0.75}$/day) calculated from the nonfasting, resting metabolic rate of this species at thermoneutrality (MacArthur and Krause 1989) and are consistent with our observation that muskrat were relatively inactive during most digestion trials.

MANAGEMENT IMPLICATIONS

The mean daily food consumption of animals in this study (577 ± 26 g/kg body mass, range 288–820 g/kg) is close to the average spring and fall requirements (734 g/kg) previously reported for captive muskrat fed natural diets (Ching and Chih-Tang 1965). Assuming muskrats waste 2–3 times as much vegetation as they consume (Takos 1947, Pelikán et al. 1970), we estimate that a minimum of 1.7–2.3 kg vegetation/kg body mass would be harvested by these rodents daily. However, if we assume a daily energy expenditure in the field equivalent to 2.65 times resting metabolic rate (Karasov 1992), the estimate is increased to 4.6–6.1 kg vegetation/kg/day. This value is comparable with that (4.2–5.6 kg vegetation/kg/day) calculated by Pelikán et al. (1970), who assumed a daily consumption rate of 1.4 kg wet vegetation/kg body mass. If the primary production of a marsh is

known, the above harvest estimates may be applied to assess the impact of resident muskrat on emergent vegetation. Because the level of forage intake was similar for all diets tested, our findings suggest that these estimates can be applied to a wide range of emergent plant communities.

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