Seasonal Changes in Gut Mass, Forage Digestibility, and Nutrient Selection of Wild Muskrats (*Ondatra zibethicus*)

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Abstract

The aim of this study was to determine whether seasonal variability in diet quality or cold stress is accompanied by compensatory changes in nutrient selection, energy intake, and digestive capacity of seasonally acclimatized muskrats. We hypothesized that in summer, muskrats meet their energy and nutrient requirements by selectively consuming high-protein, low-fiber aquatic plants. We also predicted that muskrats use fiber as an important energy source during those periods of the year when the nutritional value and diversity of forage species are lowest. At such times, muskrats should be most dependent on microbial fermentation and should exhibit maximal gut size and digestive efficiency. As predicted, muskrats offered natural forage increased the fraction of protein while reducing the proportion of fiber in their diet during summer, but not during spring or winter digestibility trials. From July to December, muskrats exhibited increases in dry matter intake, gut mass, and forage digestibility. The increase in hindgut mass was accompanied by an 18.5% rise in neutral detergent fiber digestibility, while the proportion of digestible energy derived from the fermentation of fiber increased from 38.4% in July to 53.2% in December. During winter, muskrats were able to reduce their dietary nitrogen requirements by 26.0%. Our results suggest that changes in the absorptive surface area and volume of the gut are important adaptations for promoting nutrient assimilation during periods when muskrats are challenged by both high maintenance costs and a limited choice of diets.

Introduction

The high metabolic rate to gut capacity ratio of small herbivorous mammals dictates a high energy intake, especially during periods of reproductive

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activity or low environmental temperature (Demment and Van Soest 1985). In nature, the quality and availability of principal food items also change throughout the year (Hammond 1993). Small herbivorous mammals have several options for maximizing energy and nutrient assimilation when thermoregulatory costs are high and forage quality or availability is reduced. One is to optimize forage intake and retention time, allowing the gut to operate at, or near, maximum capacity (Sibly 1981). However, on poor-quality forage, increasing the level of food intake or digesta retention time may not be sufficient to meet metabolic demands (Justice and Smith 1992; Hammond 1993). Selective consumption of high-quality, low-fiber foods may also attenuate nutritional stress, although such foods must be available in adequate quantities (Justice and Smith 1992; Hammond 1993). A third option involves phenotypic adjustments to increase the surface area and volume of the absorptive region of the gut (Derting and Bogue 1993; Hammond 1993). These changes could involve villus hypertrophy or gut hyperplasia (Brugger 1991), responses that theoretically should offset the loss of assimilation efficiency resulting from increased rates of forage intake.

In recent years, numerous laboratory studies have correlated changes in intestinal morphology with differences in reproductive status, temperature, and food quality or quantity (see Miller et al. 1990; Hammond and Wunder 1991). However, confirmation of these results for natural populations is generally lacking (Korn 1992).

In response to these needs, we initiated a study to determine whether seasonal variability in diet quality or cold stress is accompanied by compensatory changes in diet selection, daily energy intake, and digestive capacity of wild muskrats (*Ondatra zibethicus*). We hypothesized that the high thermoregulatory costs of aquatic foraging (MacArthur 1984) have led to selection in this species for high energy and nutrient assimilation from aquatic vegetation. We expected muskrats to use fiber as an important energy source during those periods of the year when high-quality, low-fiber foods are unavailable. We also predicted that during summer, energy needs would be largely met by selective consumption of low-fiber, high-protein forage, thus reducing the muskrat's dependence on microbial fermentation.

During late autumn, the translocation of nutrients from plant shoots to underground root structures, coupled with the establishment of persistent ice cover, physically limits the foraging range of this rodent while increasing the cost of feeding. We therefore hypothesized that muskrats enhance their forage assimilation capabilities in winter by increasing the size and absorptive capacity of the gut. An earlier study of laboratory-acclimated muskrats tested in early autumn (Campbell and MacArthur 1994) revealed that these animals require reduced levels of dietary nitrogen on a 100% cattail (*Typha*

latifolia) rhizome diet. As cattail rhizomes are the principal constituent of the muskrat's winter diet (Takos 1947; Jelinski 1989), we hypothesized that a similar decline in dietary nitrogen requirements occurs in winter-acclimatized muskrats.

Material and Methods

Animals

Ninety-four muskrats were livetrapped at Oak Hammock Marsh, Manitoba (50°06′ N, 97°07′ W), between May 8, 1991, and April 17, 1992. Animals were immediately transported to the Animal Holding Facility, University of Manitoba, and housed individually at 14° ± 1°C with a 12L:12D photoperiod (MacArthur 1979). Experiments were performed during each of six test periods (n = number of animals tested): May 8–June 8 (n = 17), July 3–28 (n = 17), September 9–October 1 (n = 18), November 20–December 13 (n = 18), January 27–February 17 (n = 12), and April 8–17 (n = 12). We followed a university-approved animal welfare protocol (C91-50) while conducting this experiment.

Digestibility Trials and Composition of Experimental Diets

A total of 32 digestibility and food intake trials were completed during the four test periods between May and December (n = 8 per period), and each animal was tested only once. However, one muskrat from the December digestibility trials was excluded from the analyses, since it exhibited low forage intake and lost over 10% of its body mass. Each digestibility trial was initiated on the day after animal capture and consisted of a 5-d pretrial session when the muskrat adjusted to the test ration and digestion cage, followed by a 5-d fecal and urine collection period (Campbell and MacArthur 1994). Ration composition for each test period was based on field analyses of muskrat feeding sites and estimates of forage availability in Oak Hammock Marsh (Takos 1947). Feeding sites were closely examined, and the proportion of each plant species present was recorded. For convenience, ration mixtures were rounded to the nearest 5% (fresh mass) for each plant type. During the 5-d pretrial periods, uneaten portions (orts) were examined to confirm ration selection choices. The experimental ration in May consisted of 50% cattail shoot, 25% cattail rhizome, 20% bladderwort (*Utricularia vulgaris*), and 5% sedge (*Carex atherodes*) shoot. In July, muskrats were fed a ration consisting of 70% cattail shoot, 10% cattail rhizome, and 5% each of soft-stem bulrush (*Scirpus validus*) shoot, whitetop (*Scolocholoa*

festucacea) shoot, sedge shoot, and duckweed (*Lemna minor*). The September ration consisted of cattail rhizomes (60%), cattail shoots (30%), and whitetop shoots (10%). Vegetation for digestibility trials was harvested on the day preceding each pretrial and trial session and stored at 5°C. In December, muskrats were presented with a 100% cattail rhizome ration collected in late fall, just prior to the establishment of persistent ice cover. These rhizomes were allowed to air dry, then packed in peat moss and stored at 3°C until used. Subsequent analyses of stored rhizomes showed minimal degradation of these samples between late October and mid-December.

All ration, ort, and fecal samples were analyzed for ash, protein (Kjeldahl N × 6.25), and energy in accordance with the procedures of Campbell and MacArthur (1994). Due to the high starch content of some dietary components, acid detergent fiber and neutral detergent fiber were determined by a modified Van Soest technique (Goering and Van Soest 1970) with Termamyl 120L (Åman and Hesselman 1984). Lyophilized urine samples were analyzed for nitrogen and energy content only. Calculations of apparent digestibility coefficients followed Campbell and MacArthur (1994).

Food Intake and Selectivity

To test for behavioral selection of specific dietary constituents, we subtracted the level of ash, energy, crude protein, neutral detergent fiber, and acid detergent fiber in the ration offered to muskrats from that in the remaining orts. Thus, intake for each dietary component was estimated as component in ration (%) × food offered (g) − component in orts (%) × orts (g).

The mass of each component consumed was divided by dry matter intake to calculate the fraction of that component in the diet, and this value was then compared against ration levels. The intake of daily digestible energy derived from the microbial fermentation of consumed acid detergent fiber or neutral detergent fiber was calculated, in accordance with Hammond and Wunder (1991).

Gut Morphology

All food was removed at 0900 hours on the day following completion of digestibility trials. Animals were killed at 1200–1300 hours with an overdose of Halothane anesthetic (M.T.C. Pharmaceuticals), weighed, and their gastrointestinal tracts removed, separated, and cleared of mesentery. Lengths of the stomach, small intestine, cecum, and large intestine were recorded to the nearest 1 mm by suspending each organ vertically along a meter rule.

Gut contents were removed by rinsing with physiological saline, and isolated gut segments were stored at −20°C. Digestive organs were freeze dried (72 h) and weighed to the nearest 0.1 mg on an analytical balance (Mettler model AJ100).

To determine whether acclimation during digestibility trials affected gut morphology, 9–10 additional (control) animals were livetrapped during each test period, and all measurements except digestibility were recorded from these muskrats within 2 d of capture.

Statistics

Proportions of dietary nutrients offered to, and selectively consumed by, muskrats within each season were compared by paired *t*-tests. All gut morphology variables were compared for males versus females, adults versus juveniles, and digestibility trial versus control animals, by two-way ANCOVAs with ingesta-free body mass as the covariate (SAS Institute 1990). These comparisons enabled us to determine which variables could be pooled. We evaluated seasonal diet and animal effects on body mass, food intake, digestibility, and energy and nitrogen partitioning using two-way ANOVAs. All seasonal differences between means were tested by Tukey's Studentized range test. Significance was set at the 5% level, and means are presented ±1 SE.

Results

There were no significant effects of sex, age class, or acclimation on any morphological variable involving the total gut, stomach, small intestine, or cecum ($P > 0.05$). For these variables, data for different sexes, age classes, and test groups (digestibility trials and controls) were therefore pooled. The dry mass of the large intestine was, however, greater in females than in males ($F_{1,42} = 5.13$, $P = 0.0295$) and greater in juveniles than in adults ($F_{1,61} = 4.19$, $P = 0.0456$).

Diet Selectivity

Muskrats selectively consumed specific components in the rations offered during each of the four test periods (Table 1). In May, the energy content of the food ingested was 3.8% (630 J/g dry matter intake) above that measured in the ration offered ($P = 0.0052$). During the same period, muskrats reduced ash intake 22.9% below the ration value (85.4 mg/g dry matter

TABLE 1

Nutrient composition of experimental rations offered to and selectively consumed by muskrats

	Ash (%)	Energy Content (kJ/g)	Crude Protein (%)	Neutral Detergent Fiber (%)	Acid Detergent Fiber (%)
May:					
Ration offered	11.08 (.20)	16.62 (.08)	11.39 (.27)	59.47 (1.35)	31.81 (1.69)
Diet consumed	8.54 (.48)	17.25 (.17)	11.30 (.29)	59.88 (1.90)	27.23 (1.76)
Significance of comparison between ration and diet	***	*	NS	NS	NS
July:					
Ration offered	10.54 (.04)	16.59 (.01)	6.58 (.12)	62.44 (.14)	36.62 (.09)
Diet consumed	11.83 (.33)	16.48 (.09)	8.96 (.28)	50.95 (1.13)	26.51 (.85)
Significance of comparison between ration and diet	**	NS	***	***	***

September:					
Ration offered	6.68 (.21)	17.02 (.06)	5.92 (.04)	52.25 (.56)	27.29 (.00)
Diet consumed	5.60 (.51)	17.18 (.19)	7.66 (.32)	49.81 (3.35)	23.61 (1.38)
Significance of comparison between ration and diet	NS	NS	***	NS	*
December:					
Ration offered	7.75 (.07)	16.74 (.01)	7.84 (.04)	43.33 (.62)	22.96 (.07)
Diet consumed	6.79 (.38)	16.83 (.05)	8.29 (.35)	49.99 (2.66)	24.77 (1.03)
Significance of comparison between ration and diet	*	NS	NS	*	NS

Note. Values are presented as mean (SE); $n = 8$ for all samples except September acid detergent fiber ($n = 4$). NS, not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

intake vs. 110.8 mg/g dry matter intake; $P = 0.0002$). Muskrats presented with a mixed ration containing 62.4% neutral detergent fiber in July reduced neutral detergent fiber consumption 18.4% below that offered ($P < 0.0001$). However, muskrats fed a 100% cattail rhizome ration in December increased neutral detergent fiber intake 15.4% over the ration value ($P = 0.029$). Muskrats presented with mixed rations increased protein intake over ration values in July and September, when ration protein content was lowest ($P < 0.0001$).

Gut Morphology

Dry Mass. The dry mass of the total gut changed significantly over the year ($F_{5,88} = 10.64$, $P < 0.0001$). It was lowest in May and July, increased in fall, and peaked in December (Fig. 1; $P < 0.05$). Changes in the dry mass of the small intestine, cecum, and large intestine accounted for most of this increase in total gut mass.

Although not statistically significant, stomach dry mass was lowest in spring and summer, and greatest in fall and winter. The dry mass of the small

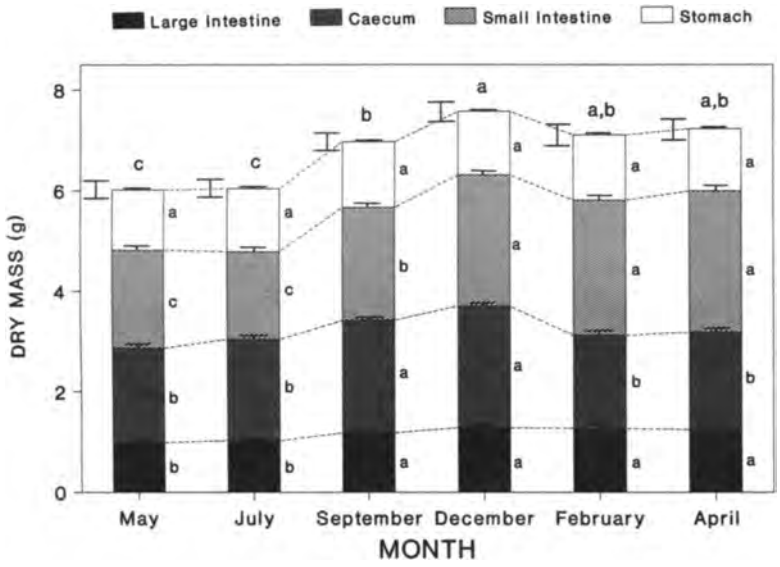

Fig. 1. Seasonal changes in the dry gut mass of 94 field-acclimatized muskrats. The error bar to the left of each histogram represents ±1 SE for the entire gut; error bars within histograms denote 1 SE for individual gut compartments (n = *12–18 animals/mo). Means sharing the same letters for individual gut segments and for the whole gut are not significantly different* (P > *0.05). Note: all means presented are adjusted means with ingesta-free body mass as the covariate.*

intestine increased from May to September ($P < 0.05$) and continued to rise throughout the winter (Fig. 1). Although not significantly different from muskrats in December and February, April-caught animals exhibited the heaviest small intestines. Cecal dry mass increased from spring to fall, reaching peak values in September and December ($P < 0.05$), and then declined to spring levels (Fig. 1). The dry mass of the large intestine was lowest in May and July ($P < 0.05$), increased from July to December, and then remained elevated until spring.

Gut Lengths. Although there were no significant changes in the lengths of the small intestine, large intestine, or total gut ($F_{5,88} = 0.74–1.37$, $P > 0.05$), these parameters were consistently highest in the December-trapped muskrats. There was seasonal variation in the lengths of the stomach ($F_{5,88} = 4.62$, $P = 0.0009$) and cecum ($F_{5,88} = 2.87$, $P = 0.0191$). Stomach length increased as winter progressed and peaked in April. Cecum length generally increased from summer to midwinter but then declined from December to February ($P < 0.05$).

Digestibility Trials

Intake. During May and July, dry matter and gross energy intake were relatively constant among animals, averaging 60 g/($kg^{0.75}$ d) and 1,011 kJ/($kg^{0.75}$ d), respectively (Table 2). However, muskrats increased dry matter intake by 26.2% and gross energy intake by 27.3% in the September and December digestibility trials ($P < 0.01$). Fecal energy output showed no definite trend, although it was highest in May and September. Urinary energy loss increased from May to July ($P < 0.05$) but then declined sharply in September and December, when it was less than 25% of July values.

Apparent Digestibility. The digestible energy and metabolizable energy coefficients of muskrats tested in December were higher than for muskrats tested in May but not higher than for muskrats tested July and September (Table 2). Neutral detergent fiber and acid detergent fiber digestibilities were highest in December. Digestibility of the neutral detergent soluble fraction was highest in July, although not significantly greater than in December or September. Crude protein digestibility was highly variable, ranging from a minimum of 15.35% in September to a maximum of 38.37% in July (Table 2).

Intake and Partitioning of Dietary Nitrogen

The mean daily nitrogen intake of muskrats was similar throughout the year ($F_{3,27} = 2.86$, $P = 0.056$), ranging from 0.86 g/$kg^{0.75}$ in July to 1.08 g/$kg^{0.75}$

TABLE 2

Effects of season and diet on food intake, digestibility, and energy gain of field-acclimatized muskrats

	May (n = 8)	July (n = 8)	September (n = 8)	December (n = 7)
Body mass (g)	1,000[a] (27)	901[a,b] (37)	1,010[a] (50)	826[b] (44)
Dry matter intake (g/[kg$^{0.75}$ d])	59.72[b] (2.61)	60.30[b] (1.74)	75.87[a] (3.06)	75.55[a] (5.95)
Digestibility (%):				
Dry matter	44.39[c] (2.50)	54.82[a,b] (2.37)	49.23[b,c] (2.09)	59.84[a] (3.16)
Digestible energy	41.61[b] (2.41)	52.70[a] (2.29)	46.98[a,b] (1.86)	55.96[a] (3.32)
Metabolizable energy	39.08[b] (2.50)	48.86[a] (2.26)	46.53[a,b] (.94)	54.89[a] (3.30)
Crude protein	25.81[a,b] (3.08)	38.37[a] (2.88)	15.35[b] (5.04)	21.66[b] (5.37)
Neutral detergent solubles	48.92[b] (4.22)	70.02[a] (1.52)	55.73[a,b] (4.85)	59.05[a,b] (6.10)
Neutral detergent fiber	40.65[b] (2.05)	40.15[b] (3.05)	38.76[b] (4.73)	58.60[a] (2.30)
Acid detergent fiber	34.10[b,] (3.66)	29.07[b] (4.06)	41.03[b,*] (6.05)	62.77[a] (2.07)
Energy gained (kJ/[kg$^{0.75}$ d]):				
Gross energy	1,027.6[b] (37.6)	993.5[b] (27.9)	1,303.9[a] (57.1)	1,269.3[a] (98.0)
Metabolizable energy	406.0[c] (35.1)	482.9[b,c] (19.6)	599.7[a,b] (11.3)	706.9[a] (78.0)
Digestible energy	431.5[c] (34.8)	520.9[b,c] (19.6)	605.8[a,b] (11.0)	721.3[a] (86.2)
Neutral detergent fiber	249.9[a,b] (17.5)	201.1[b] (14.1)	259.1[a,b] (46.6)	360.7[a] (25.3)
Neutral detergent solubles	210.6[b] (28.7)	341.1[a,b] (13.5)	375.5[a,b] (49.8)	409.3[a] (76.9)
Acid detergent fiber	97.9[b] (14.4)	76.7[b] (11.1)	134.1[a,b,*] (24.9)	199.3[a] (21.0)

Note. Values are presented as mean (SE). Within each row, means sharing the same letter are not significantly different ($P > 0.05$).

* n = 4.

in May (Table 3). Mean fecal nitrogen loss was similar for May, September, and December trials, but was reduced in July. In contrast, mean urinary nitrogen loss was 16.5 times greater in July than in September (Table 3). This component of nitrogen loss closely paralleled urinary energy loss in that it remained high in spring and summer before dramatically falling in autumn. Regressing tissue nitrogen balance on daily nitrogen intake (Campbell and MacArthur 1994) revealed two distinct seasonal models; for May and July, TNB = −1.300 + 1.189 DNI, where TNB is tissue nitrogen balance and DNI is daily nitrogen intake (r^2 = 0.69, df = 14), and for September and December, TNB = −0.561 + 0.691 DNI (r^2 = 0.62, df = 14). These models predict that the minimum daily nitrogen intake required to meet tissue nitrogen balance is lower in fall and winter (0.811 g/[$kg^{0.75}$ d]) than in spring and summer (1.091 g/[$kg^{0.75}$ d]).

Discussion

Seasonal Changes in Gut Morphology and Digestive Efficiency

Laboratory studies have established that small endotherms can dramatically alter the size and absorptive capacities of specific regions of the gastrointestinal tract in response to changes in fiber content, reproductive status, and temperature. For instance, voles exposed to low temperatures increase forage intake and the size of the small intestine, which results in greater

TABLE 3
Seasonal intake and partitioning of dietary nitrogen in field-acclimatized muskrats

Variable (g/[$kg^{0.75}$ d])	May (n = 8)	July (n = 8)	September (n = 8)	December (n = 7)
Nitrogen intake	1.08[a] (.04)	.86[b] (.02)	.93[a,b] (.06)	.97[a,b] (.08)
Fecal nitrogen	.79[a] (.02)	.53[b] (.03)	.77[a] (.03)	.74[a] (.03)
Urinary nitrogen	.25[b] (.02)	.66[a] (.03)	.04[c] (.01)	.12[c] (.03)
Nitrogen balance	.03[a] (.02)	−.32[b] (.03)	.12[a] (.06)	.11[a] (.06)
Apparent digestible nitrogen	.28[a] (.04)	.33[a] (.03)	.16[a] (.06)	.23[a] (.07)

Note. Values are presented as mean (SE). Within each row, means sharing the same letter are not significantly different ($P > 0.05$).

energy absorption (Gross et al. 1985; Hammond and Wunder 1991). Similarly, small herbivores presented with rations of low quality (increased fiber) have been shown to increase forage intake as well as the volume and surface area of the cecum and large intestine (Hammond and Wunder 1991; Loeb et al. 1991). However, few studies (Miller et al. 1990; Hammond 1993) have demonstrated that similar modifications in gut size or absorptive capacity occur in wild populations. Our findings clearly indicate that gut size and forage digestibility of free-ranging muskrats do not remain static, but vary seasonally, likely in response to temporal changes in energy demand and fiber intake. It is important to recognize that muskrats in this study were fed natural diets that varied with season. Therefore, we could not clearly distinguish dietary effects from other factors that might have contributed to the observed seasonal trends in gut size and digestive function. The observed changes in gut mass could not be attributed to changes in the composition of this tissue, since the wet to dry mass ratio of the gastrointestinal tract showed little seasonal variation. Furthermore, we observed little correspondence between gut mass and changes in body composition (i.e., fat content) during summer or late winter (K. L. Campbell and R. A. MacArthur, unpublished observation).

Muskrats undergo a significant reduction in the mass of intestinal tissue and body fat reserves between April and May (Virgl and Messier 1992; this study). During the breeding season, males experience a more rapid decline in body fat stores than females, a trend that may reflect the high cost of establishing male breeding territories (Virgl and Messier 1992). As gut tissue is metabolically expensive to maintain (Brugger 1991), it may be adaptive for males to reduce intestinal mass and mobilize surplus fat reserves in early spring. Unfortunately, no females were collected during the breeding season in this study. Virgl and Messier (1992) reported that female muskrats have larger digestive tracts than males from June through August. It is likely that the females in our study population also maintained larger guts in response to the high costs of pregnancy and lactation.

Muskrats collected in July demonstrated no appreciable change in total gut mass, gut length, or dry matter intake, compared to spring-caught animals. However, digestive efficiencies were consistently higher in July. The presence of secondary plant compounds and structural digestion inhibitors is known to reduce digestibility of forages consumed by small herbivores (Robbins 1993), and many mammals appear to select foods on the basis of levels of digestive inhibitors (Miller et al. 1990). Seasonal variability in lignin concentration of the experimental rations was small (range: 3.22%–4.97%), and it is unlikely that these differences led to the changes in fiber use and digestibility that we observed. Although it is conceivable that as-

sociative digestion effects may have influenced our forage digestibility estimates, results of a previous study (Campbell and MacArthur 1994) suggest that these factors were generally insignificant.

Small herbivores are expected to prefer foods that can be rapidly absorbed and are low in fiber (Loeb et al. 1991), and we believe the high digestibility values recorded during July are mainly the result of forage selection. Muskrats presented with a mixed ration containing 62.4% neutral detergent fiber and 6.58% protein in July selectively consumed vegetation containing only 51.0% neutral detergent fiber (18.4% below ration level) but 8.96% protein (36.2% above ration level; Table 1). Evidently, muskrats in summer are able to meet their energy needs by selectively consuming lower levels of fiber, rather than by increasing gut mass. Selective feeding reduces the dependence of many small herbivores on microbial fermentation (Justice and Smith 1992). Indeed, the fraction of energy derived from this source declined from 59.5% of digestible energy intake in May to 38.4% in July (Table 2). It is noteworthy that the latter value is still well above previously reported estimates for other small herbivores maintained on high-fiber rations. Prairie voles (*Microtus ochrogaster*), wood rats (*Neotoma* spp.), and collared lemmings (*Dicrostonyx groenlandicus*) obtained only 19%–32% of digestible energy from rations containing 39%–49% neutral detergent fiber (Hammond and Wunder 1991; Justice and Smith 1992; Nagy and Negus 1993).

Our data suggest that the muskrat's ability to digest fiber actually exceeds predictions based on body mass. According to the computer simulations of Justice and Smith (1992), a 1-kg herbivore fed an alfalfa-based ration containing 60% neutral detergent fiber should exhibit a neutral detergent fiber digestibility of 24% and obtain 33% of its digestible energy through microbial fermentation. In May, muskrats consuming a mixed ration containing 59.9% neutral detergent fiber displayed a neutral detergent fiber digestibility of 40.7% while obtaining 59.5% of their digestible energy from fiber. According to the model developed by Justice and Smith (1992), our fiber use values correspond to those predicted for a 20-kg animal. We believe our values represent a conservative estimate of fiber digestibility in muskrats, since cecum mass was lowest in spring (Fig. 1). These findings are in accord with an earlier study (Campbell and MacArthur 1994) indicating that muskrats readily adapt to high-fiber diets and use these structural carbohydrates as an important energy source.

An increased cecal capacity permits a larger volume of fermentable particles to be retained in the gut and hence provides more time for microbial fermentation. The muskrat possesses a large haustrated cecum which empties into a complex (eight-spiral) proximal colon (Luppa 1957) similar to that described for the Scandinavian lemming, *Lemmus lemmus* (Vorontsov 1967).

Sperber et al. (1983) have shown that the convolutions of the lemming's proximal colon create a separation mechanism that traps and provides for a direct flow of bacteria and fine particles back towards the cecum. Selective retention of fluid and small particles in the cecum should permit more complete digestion of dry matter, since fine particles have an increased fermentable surface area and will support a higher concentration of bacteria.

In muskrats, the dry masses of the total gastrointestinal tract, small intestine, cecum, and large intestine had all increased by September. Despite these gains, digestive efficiencies were slightly lower in September than in July (Table 2). Since neutral detergent fiber levels of the ingested diet were similar for both months, the small reduction in digestibilities of dry matter, digestible energy, and metabolizable energy in September are likely a response to the 25.8% increase in daily dry matter intake ($g/kg^{0.75}$). As pointed out by Robbins (1993), reduced digestibility need not be maladaptive if it leads to an increase in total nutrient absorption. Indeed, results for the September digestibility trial indicated that muskrats increased their daily metabolizable energy intake 24.2% over July values (Table 2). This gain in energy absorption is likely linked to the increase in small intestine mass, and the continued enlargement of this organ during fall and winter probably served to facilitate further extraction of easily digestible nutrients from the diet (e.g., neutral detergent solubles and protein).

The notable increases in dry mass of the cecum and large intestine between July and September are presumably the consequence of increased dry matter intake, since the neutral detergent fiber content of ingested forage remained close to 50% (Table 1). It appears paradoxical that the 11% gain in cecal dry mass from July to September was correlated with a 1.5% decrease in neutral detergent fiber digestibility. However, over the same period, the proportion of daily energy gained from the fermentation of neutral detergent fiber and acid detergent fiber increased 4.2% and 7.5%, respectively. It is of interest that December-trapped animals fed a 100% cattail rhizome ration consumed portions of the rhizomes that were high in fiber (15% above ration offered). Consequently, December-caught muskrats consumed, on average, the same amount of fiber as animals trapped in September (37.8 $g/[kg^{0.75}\ d]$). However, the 8% gain in cecal mass of muskrats in December appeared to increase both their neutral detergent fiber digestibility (from 38.76% to 58.60%) and the proportion of digestible energy derived from neutral detergent fiber (from 42.56% to 53.23%).

Muskrats begin accumulating body fat stores in September (Virgl and Messier 1992; K. L. Campbell and R. A. MacArthur, unpublished observations), presumably to offset potential food shortages in late winter. Dry masses of the total gut, cecum, and large intestine peaked in December-

trapped muskrats, and we interpret this as a mechanism to maximize energy absorption and the accumulation of body lipid reserves. The observed gains in gut mass probably also contributed to the substantial increases in digestibilities (10%–20%) for the dry matter, digestible energy, metabolizable energy, neutral detergent fiber, and acid detergent fiber components from September to December (Table 2).

It is possible that there has been strong selective pressure for muskrats to maximize energy derived from cattail rhizomes, which account for a large proportion of the muskrat's winter diet (Takos 1947). Our results support this hypothesis, as muskrats in December were able to increase metabolizable energy intake by 17.9% over September values, even though gross energy intake was 2.7% lower. We similarly reported a high dry matter digestibility (70.6%) and metabolizable energy intake (521.4 kJ/[$kg^{0.75}$ d]) in an earlier study of laboratory-acclimated muskrats consuming a 100% cattail rhizome diet (Campbell and MacArthur 1994).

Seasonal Nitrogen Dynamics

Since nitrogen is often a limiting nutrient in the diet of herbivores, its digestibility and retention are crucial (Loeb et al. 1991). Our findings suggest that the minimum nitrogen intake required to meet tissue nitrogen balance is 0.280 g/($kg^{0.75}$ d) less in fall and winter than during spring and summer. In a previous study (Campbell and MacArthur 1994) we reported a similar reduction in the nitrogen requirements of muskrats maintained on a 100% cattail rhizome ration in late summer and early fall. Furthermore, muskrats in the present study were able to maintain tissue nitrogen balance in September and December (Table 3) on diets containing only 8% protein. This value is only half that generally recognized as constituting a minimal requirement in rodent diets (Jelinski 1989).

It is possible that muskrats may, like some hibernators (Steffen et al. 1980; Bintz and Torgerson 1981), conserve body nitrogen in winter by reducing urinary nitrogen output through urea recycling. The recycling of urea formed from tissue nitrogen may be important to the nitrogen economy of animals when nitrogen intake is inadequate to meet daily requirements (Robbins et al. 1974).

The large cecum, selective increase in dietary fiber intake, and possibly the recycling of nitrogen may all contribute to maintaining intestinal bacteria and protozoan populations in winter. Furthermore, muskrats are known to practice coprophagy (K. L. Campbell, unpublished observations), but no steps were taken to either prevent or quantify this behavior in the present study. Thus, it is conceivable that coprophagy not only may have contributed

to the high fiber digestibilities reported herein, but may, along with urea recycling, be an important mechanism used by muskrats to meet their seasonal nitrogen requirements.

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