DIGESTIBILITY OF ANIMAL TISSUE BY MUSKRATS

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We examined the potential nutritional benefits derived by muskrats (*Ondatra zibethicus*) that supplement their diet of aquatic plants with animal tissue. Digestibility, energy, and nitrogen-balance trials were conducted with adult muskrats fed each of three diets: 100% shoots of cattails (*Typha latifolia*); 95% shoots of cattails, 2.5% fathead minnows (*Pimephales promelas*), and 2.5% flesh of muskrats; 85% shoots of cattails, 10% fathead minnows, and 5% flesh of muskrats. Muskrats presented with diets containing meat selectively increased the proportion of animal tissue ingested above that offered in the ration ($P < 0.001$). Gain in body mass, intake of dry matter, and coefficients of dry matter, energy, and protein digestibility all increased with rising levels of consumption of meat. Our results demonstrate that muskrats can efficiently digest high levels of animal tissue (>50% intake of dry matter) with no apparent loss of ability to digest fiber. They further suggest that free-ranging muskrats consuming diets containing only 2–3.5% animal tissue can meet their maintenance requirements of daily nitrogen (1.02 g N/kg$^{0.75}$ body mass) solely from meat. We conclude that consumption of meat, even at low levels, can be nutritionally beneficial to muskrats in nature.

Key words: Muskrat, *Ondatra zibethicus,* digestibility, carnivory, herbivory, nitrogen, nutrition, Manitoba

Protein often is assumed to constitute a primary dietary constraint limiting the growth and reproduction of mammalian herbivores (Loeb et al., 1991; Robbins, 1993). Seasonal deficiencies in dietary protein may be compounded by the high fiber content of mature plants, thus reducing the amount of readily digestible energy that small herbivores can extract from such diets (Hammond, 1993).

The muskrat (*Ondatra zibethicus*) feeds predominantly on aquatic plants that are high in fiber and low in nitrogen (Campbell and MacArthur, 1994). Previous digestion trials (Campbell and MacArthur, 1994, in press) suggested that muskrats consuming diets composed solely of aquatic vegetation have difficulty maintaining nitrogen balance in summer. How free-ranging muskrats meet their daily nitrogen requirements is unknown. One possibility involves the opportunistic feeding on concentrated nitrogen sources such as animal matter, which may help to alleviate seasonal deficiencies of crude protein in the diet (Karasov, 1982).

The consumption of animal tissue, including flesh of muskrats, often has been reported in studies of food preference of *O. zibethicus* (Convey et al., 1989; Errington, 1941; Neves and Odom, 1989; Stearns and Goodwin, 1941; Triplet, 1983). Ching and Chih-Tang (1965), e.g., reported that animal tissue accounted for 6.6% of the daily food intake by muskrats. Unfortunately, the nutritional benefits of this dietary component are poorly understood, because little is known regarding the digestibility and assimilation of animal flesh by mammalian herbivores.

In response to these needs, we initiated a study to evaluate the potential nutritional benefits of ingestion of tissue by muskrats, specifically in terms of energy and nitrogen balance. We hypothesized that muskrats, when presented with a choice, would actively select a diet containing a higher level of animal tissue than that offered in a mixed

TABLE 1.—*Nutrient composition of the three food items fed to muskrats in feeding trials conducted at the University of Manitoba, 9 June–14 August 1993. Means ± 1 SE are indicated.*

Food item	*n*	Shoots of cattails	Fathead minnows	Flesh of muskrats
Dry matter (%)	30	6.0 ± 0.2	19.4 ± 0.2	24.9 ± 0.4
Energy (KJ/g)	12	15.7 ± 0.7	20.7 ± 0.1	23.4 ± 0.2
Crude protein (%)	12	13.2 ± 2.5	65.7 ± 0.9	82.7 ± 2.2
Neutral detergent fiber (%)	12	51.7 ± 0.9		
Ash (%)	12	16.4 ± 0.5	14.6 ± 0.3	4.6 ± 0.1

ration containing aquatic vegetation and vertebrate animal matter. We also predicted that coefficients for digestibility of dry matter, energy assimilation, and nitrogen retention would all increase with rising levels of consumption of meat by muskrats.

MATERIALS AND METHODS

Eight adult male muskrats were captured at Oak Hammock Marsh, Manitoba (50°06′N, 97°07′W) in mid-May 1993. Animals were housed individually in a walk-in environmental chamber kept at 14 ± 1°C with a photoperiod of 12L:12D (MacArthur, 1979). Except during digestion trials, muskrats were fed rodent chow (Agway Prolab, Syracuse, NY) supplemented with apples and carrots. All animals were acclimated to laboratory holding facilities for a minimum of 3 weeks before initiation of digestion trials. A university approved animal welfare protocol was followed while conducting this experiment.

A total of 24 digestibility and food-intake trials were completed during six periods between 9 June and 14 August 1993. Muskrats were tested once on each of three rations and the order of presentation of rations was randomized. Consecutive tests on the same individual were separated by a minimum of 14 days. Each digestion trial lasted 5 days and was preceded by a 5-day adjustment period during which muskrats were fed the test ration. Protocol for the digestion trial, sample analyses, and calculations of coefficients of apparent digestibility followed Campbell and MacArthur (1994). Ash content was determined by combusting 2-g duplicate samples for 6 h at 600°C (Association of Official Analytical Chemists, 1984).

In all trials, muskrats were presented with a total daily ration (1,000 g) that was about twice the daily intake previously recorded for captive muskrats (Campbell and MacArthur, 1994). On a wet-weight basis, the test rations consisted of: 1) 100% shoots of cattails (*Typha latifolia*; hereafter referred to as 0% meat ration); 2) 95% shoots of cattails, 2.5% fathead minnows (*Pimephales promelas*), and 2.5% flesh of muskrats (5% meat ration); 3) 85% shoots of cattails, 10% fathead minnows, and 5% flesh of muskrats (15% meat ration). On a dry-weight basis, rations offered to muskrats consisted of 16.5% animal tissue in the 5% meat ration and 38.9% in the 15% meat ration. Cattails are the dominant food source of muskrats in marshes of the northern prairie (Campbell and MacArthur, 1994), and flesh of muskrats and fathead minnows are forms of animal tissue available to populations of muskrats in Oak Hammock Marsh. These rations also were selected to provide ranges of protein and energy availability (Table 1) that might be encountered by muskrats in nature.

Shoots of cattails were harvested at Oak Hammock Marsh on the day before each pretrial and trial session. Minnows were collected from a retention pond near the University of Manitoba, rinsed, and frozen whole in sealed plastic bags at −20°C. Skeletal muscle was removed from previously frozen carcasses of muskrats and was similarly stored at −20°C. All tissues were thawed immediately before presenting rations to muskrats.

Ration and animal effects were evaluated using the general-linear-models procedure of SAS (Sas Institute, Inc., 1990), and treatment means were compared with *t*-tests for pairwise comparison of least-squares means, with significance set at 0.017 (0.05/3 treatments) to correct for multiple comparisons. Proportions of food items in rations offered to, and in diets consumed by muskrats were compared using paired *t*-tests. Predictive equations were derived by least-squares regression analysis. All means are presented ±1 *SE*.

TABLE 2.—*Proportions of food items (dry weight basis) offered to, and selectively consumed by muskrats in feeding trials conducted at the University of Manitoba, 9 June–14 August 1993. Means ± 1 SE and number of trials (in parentheses) are indicated.*

Food item	5% meat in ration (n = 8)	15% meat in ration (n = 7)
Shoots of cattail		
Ration offered (%)	83.5 ± 0.6	61.1 ± 1.1
Diet consumed (%)	69.7 ± 2.0	40.7 ± 1.3
	$P < 0.001$[a]	$P < 0.001$
Whole fish		
Ration offered (%)	7.3 ± 0.2	26.3 ± 1.4
Diet consumed (%)	14.1 ± 1.3	38.6 ± 3.3
	$P < 0.001$	$P = 0.005$
Flesh of muskrats		
Ration offered (%)	9.2 ± 0.4	12.6 ± 1.5
Diet consumed (%)	16.2 ± 0.9	20.7 ± 3.3
	$P < 0.001$	$P = 0.044$

[a] P-value for paired t-test comparing the proportion of a food item offered in the ration and the proportion of that same food item in the diet actually consumed by muskrats.

RESULTS

In 15 of the 16 digestibility trials involving animal tissue, muskrats consumed a higher proportion of meat than was initially offered in the test rations (Table 2, $P < 0.001$). This selectivity resulted in muskrats ingesting diets that consisted of 30.3% (5% meat ration) and 59.3% (15% meat ration) animal tissue on a dry-weight basis (Table 2). One muskrat on the 15% meat ration consumed animal tissue at a level slightly below that offered in the diet. This individual was subsequently excluded from the analyses because its consumption of tissue was 18–28% lower than that of other animals on the 15% meat ration.

Body mass and energy intake of muskrats increased with rising levels of consumption of meat (Table 3). Intake of metabolizable energy was more than two times greater on the 15% meat ration than on the 0% meat ration ($P < 0.001$). Similarly, intake of dry matter was 59% higher on the 15% meat ration than on the 0% meat ration (Table 3, $P < 0.001$). Despite the progres-

TABLE 3.—*Body mass, energy intake, and apparent digestibilities of adult male muskrats maintained on three diets differing in proportion of animal tissue. Feeding trials were conducted at the University of Manitoba, 9 June–14 August 1993. Means ± 1 SE and number of trials (in parentheses) are indicated.*[a]

Variable	0% meat in ration (n = 8)	5% meat in ration (n = 8)	15% meat in ration (n = 7)
Body mass (g)[b]	911.5 ± 33.7A	931.7 ± 33.0A	986.7 ± 37.4A
Change in mass (g)	−37.3 ± 8.7C	−4.9 ± 9.3B	29.1 ± 8.1A
Daily intake			
Dry matter ($g/kg^{0.75}$)	31.2 ± 2.2B	36.5 ± 3.2B	46.7 ± 2.9A
Gross energy ($kJ/kg^{0.75}$)	482.0 ± 35.9B	618.4 ± 60.7B	837.8 ± 65.1A
Digestible energy ($kJ/kg^{0.75}$)	310.7 ± 26.9C	477.1 ± 47.5B	698.0 ± 51.1A
Metabolizable energy ($kJ/kg^{0.75}$)	287.9 ± 25.2C	434.3 ± 47.2B	641.6 ± 53.0A
Digestibility (%)			
Dry matter	67.4 ± 1.2B	77.1 ± 2.0A	80.7 ± 1.2A
Digestible energy	64.2 ± 1.6C	82.7 ± 1.5B	89.6 ± 0.7A
Metabolizable energy	59.4 ± 1.6C	77.0 ± 1.4B	85.3 ± 0.4A
Dietary crude protein	61.9 ± 6.2B	85.6 ± 1.5A	91.2 ± 0.7A
Neutral detergent solubles	73.1 ± 1.5B	81.0 ± 1.3A	82.9 ± 1.1A
Neutral detergent fiber	57.7 ± 2.9A	66.1 ± 4.5A	67.4 ± 2.6A

[a] Within each row, means sharing same letter are not different ($P > 0.017$).

[b] Average body mass during trial.

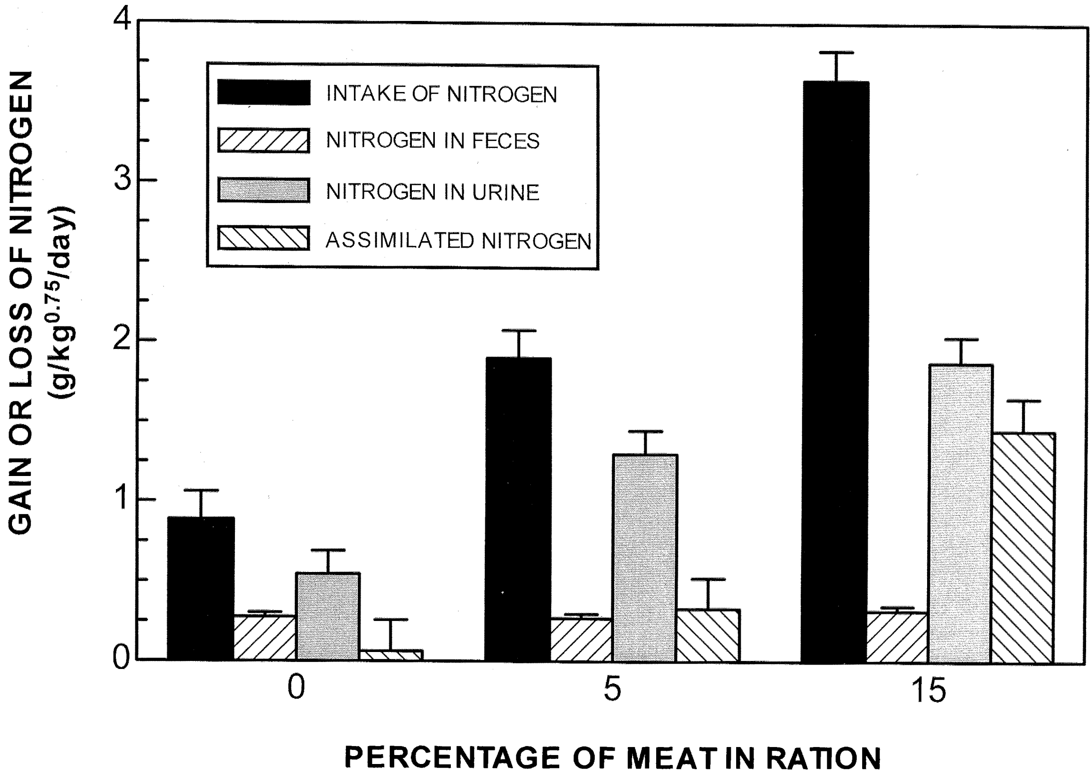

FIG. 1.—Relationship of intake of daily nitrogen to loss of nitrogen in feces, loss of nitrogen in urine, and net gain of nitrogen in muskrats fed three rations differing in proportion of animal tissue. Values are presented as means ± 1 *SE.*

sive gain in intake of dry matter, the digestibility coefficients for dry matter, digestible energy, metabolizable energy, protein, neutral detergent fiber, and neutral detergent solubles all increased with the level of meat consumption (Table 3).

As expected, daily intake of nitrogen, retention of nitrogen, and loss of urinary nitrogen increased concurrently with consumption of meat, whereas loss of fecal nitrogen varied little among diets (Fig. 1). Regressing daily nitrogen balance on daily intake of nitrogen (Campbell and MacArthur, 1994) yielded the equation: daily balance of nitrogen in tissues = −0.560 + 0.548 daily intake of nitrogen (r^2 = 0.74, *d.f.* = 23). From this regression, the maintenance requirement of muskrats for nitrogen was estimated to be 1.02 g N/kg$^{0.75}$/day.

DISCUSSION

Numerous studies published on the diets and nutrient requirements of microtine rodents indicate animal tissue contributes <10% of the total diet (Batzli, 1985). Unfortunately, little or no attention has been paid to the nutritional significance of consumption of meat by these small herbivores. Our results clearly indicate that low levels of ingestion of meat can lead to significant gains in the energy and protein absorption by muskrats. Associative effects arising from feeding herbivores mixed diets have been reported (Bjorndal, 1991), and it is possible that this phenomenon may be responsible, at least in part, for the high digestibilities we observed.

Although muskrats possess a specialized digestive tract adapted to efficiently process aquatic vegetation (pers. obs., in press), there is no evidence of morphological adaptations for handling a carnivorous diet (Luppa, 1956). Nevertheless, it appears that muskrats do not suffer any loss in digestive efficiency resulting from the consumption of animal tissue, even at high levels of ingestion (>50% intake of dry matter; Table 3). Digestibilities of dry matter and metabolizable energy of muskrats fed the 15% meat ration were 10–47% higher than those recorded for muskrats fed only diets of emergent plants (Campbell and MacArthur, 1994, in press; this study). The high digestibilities of dry matter and metabolizable energy recorded on the 15% meat ration cannot be ascribed to variation in intake of dry matter, because the range of intake of dry matter for the three diets tested in this study (31.2–46.7 g/kg$^{0.75}$/day) is similar to that (31.4–48.7 g/kg$^{0.75}$/day) reported by Campbell and MacArthur (1994). We observed no evidence that the ability of this rodent to digest plant fiber (Campbell and MacArthur, 1994, in press) is compromised by the addition of animal tissue to the diet (Table 3). Although digestibility of neutral detergent fiber was highest on the 15% meat ration, the proportion of daily intake of metabolizable energy derived from the fermentation of fiber decreased from to 51.1% (147.50 kJ/kg$^{0.75}$/day) on the 0% meat ration, to only 16.4% (106.72 kJ/kg$^{0.75}$/day) on the 15% meat ration. Muskrats on the 0% meat ration, however, ingested 39% more neutral detergent fiber than did animals on the 15% meat ration.

Our estimate of digestibility of digestible energy on the 15% meat ration (89.6 ± 0.7%) is close to the values reported for carnivores consuming meat (95.5%), fish (95.3%), and whole bird or mammal diets (85.3%; Robbins, 1993). Muskrats maintained on the 5 and 15% meat rations also exhibited apparent digestibilities of crude protein (85.6 and 91.2%, respectively) similar to those of carnivores (78.9–96.8%) fed rations of pure meat (Davidson et al., 1978; Harper et al., 1978; Powers et al., 1989). More importantly, assuming a true nitrogen digestibility of 94% (this study), our data suggest that nonreproducing adult muskrats can meet their daily nitrogen requirement for maintenance (1.02 g N/kg$^{0.75}$ body mass) from the consumption of only 31.2 g of muskrat flesh or 53.1 g of fathead minnows on a wet-weight basis. These values represent only 2–3.5% of the estimated wet mass of aquatic vegetation required each day to sustain free-ranging muskrats (ca. 1,530 g—Campbell and MacArthur, 1994). A similar pattern has been described by Karasov (1982) for the white-tailed antelope squirrel (*Ammospermophilus leucurus*), which apparently can meet its daily nitrogen requirements solely from the component of animal tissue in an omnivorous diet (8% of total intake).

The consumption of animal matter has the potential to play a major role in the nitrogen economy of muskrats (Fig. 1). This may be especially true for juveniles, because consumption of meat should enable young to maximize somatic growth, thereby achieving a larger body size at the onset of winter. Occasional consumption of meat also may benefit populations of muskrats existing in marginal habitats characterized by low-quality, protein-deficient forage (Messier et al., 1990). The question remains, however, if muskrats are so efficient at using flesh of animals as an energy and nitrogen source, why is carnivory not more prevalent among muskrats in nature? Perhaps the increased foraging time required, coupled with a greater risk of injury or predation, have selected against a stronger reliance on animal tissue in the diet of these rodents. Perhaps muskrats obtain most of their meat as scavengers, and the amount of meat in their diet varies with the availability of prey. Such opportunistic consumption of animal tissue is difficult to document in nature, and perhaps this habit is more widespread in wild populations of muskrats than previously was thought.

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