

SEASONAL CHANGES IN WATER FLUX, FORAGE INTAKE, AND ASSIMILATED ENERGY OF FREE-RANGING MUSKRATS

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Abstract: Knowledge of the seasonal energy and forage requirements of free-ranging muskrats (*Ondatra zibethicus*) is essential for evaluating the habitat requirements and potential effect of this species on aquatic vegetation. We measured rates of water influx with the deuterated water (D_2O) technique and assessed the accuracy of this method for estimating dry-matter intake (DMI) of captive muskrats fed a natural diet of cattail (*Typha latifolia*) rhizomes. Water influx in laboratory feeding trials was highly variable, ranging from 97 to 430 $mL \cdot kg^{-1} \cdot day^{-1}$ ($\bar{x} = 243.5 \pm 24.0$). Over this range, DMI estimated from water influx exceeded measured DMI by an average of 52.2%. This error was reduced substantially as water influx increased, with a mean error of only 9.2% when water influx averaged 349 $mL \cdot kg^{-1} \cdot day^{-1}$ (DMI > 40 $g \cdot kg^{-1} \cdot day^{-1}$). At rates of water influx obtained under field conditions (423–915 $mL \cdot kg^{-1} \cdot day^{-1}$), the error in estimating DMI is predicted to be <10%. We obtained 33 seasonal estimates of the daily intake of water, fresh vegetation, dry matter (DM), and assimilated energy (AE) of 27 free-ranging muskrats. Water influx and consumption of fresh vegetation were highest from spring through fall. However, because of the lower water content and higher digestibility of the winter diet, daily intake of DM and AE were higher ($P < 0.05$) in winter (76.9 $g/kg^{0.75}$, 713.1 $kJ/kg^{0.75}$) than midsummer (54.9 $g/kg^{0.75}$, 438.6 $kJ/kg^{0.75}$). If corrections are made for wastage and use of vegetation for house construction, these food consumption estimates can be used to assess the potential effect of muskrats on the primary productivity of prairie marsh ecosystems.

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The foraging and lodge construction activities of muskrats can substantially alter the vegetation structure of marsh ecosystems (Pelikán et al. 1970; Danell 1978, 1979). Consequently, several researchers have attempted to estimate the daily food consumption (Butler 1940, Ching and Chih-Tang 1965, Akkermann 1975, Campbell and MacArthur 1994) and resulting effect of muskrats on marsh vegetation (Pelikán et al. 1970). However, predictions based on studies of captive muskrats may not accurately reflect the forage requirements of wild populations, especially when these studies fail to allow for annual variation in plant phenology, diet composition, and the energy costs of free existence. In a recent study of acclimatized muskrats fed natural, mixed diets, we observed that the DMI of these rodents was >26% higher in fall and winter than during spring and summer (Campbell and MacArthur 1996). However, this was a laboratory study of penned animals; similar patterns in food consumption may not occur in wild populations.

A promising technique for estimating food intake of unrestrained animals involves the use of the biological water tracers deuterium and tritium (Robbins 1993). Deuterated water is particularly suited to field studies because it is inexpensive, nonradioactive, and relatively easy to analyze (Costa 1987, Robbins 1993). In principle, the rate of disappearance of this tracer from the body water pool can be used to estimate the water influx of animals (Lifson and McClintock 1966, Shoemaker et al. 1976, Nagy and Costa 1980). If the metabolic water production of the animal and the moisture and energy content of consumed vegetation are known and remain constant during the measurement period, then the intake of DM and AE can be estimated from measurements of water influx (Shoemaker et al. 1976, Peppard et al. 1993). This technique is most accurate when applied to species that meet all of their water requirements from the consumption of diets with high moisture contents (Shoemaker et al. 1976, Costa 1987).

The semiaquatic muskrat is ideally suited for application of the D_2O technique. Given the

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water-resistant qualities of the muskrat's pelage and the high water content (>80%) of ingested forage (Campbell and MacArthur 1994, 1996), any error associated with water exchange across the skin and lungs should be relatively minor.

The objectives of this study were 2-fold. First, we wished to assess the accuracy of the D₂O dilution method for determining forage intake of muskrats using 24- and 48-hr validation trials and, if necessary, obtain correction indices that might be applied to values obtained in the field. Muskrats have a high urine output, which reflects the high moisture content of their diet (Campbell and MacArthur 1994, 1996). Thus, there is a reasonable probability of obtaining voided urine samples at specified sampling intervals, and we investigated the possibility of using D₂O values obtained from these samples to determine total body water (TBW) and water influx of muskrats. Our second objective was to obtain reliable measures of water influx from which we could estimate the daily intake of vegetation and AE of free-ranging muskrats during different seasons. Ultimately, such data should enable researchers to refine estimates of the seasonal forage and energy requirements of muskrats, which is essential to developing a better understanding of the role of these animals in modifying marsh ecosystems (McCabe 1982). This information is also vital to the interpretation of seasonal dynamics in protein and lipid reserves of wild populations (Virgl and Messier 1992).

METHODS

Laboratory Validation Trials

We livetrapped 8 muskrats (576–1,080 g) at Oak Hammock Marsh, Manitoba, Canada (50°06'N, 97°07'W), in August 1994 and transported them to the Animal Holding Facility at the University of Manitoba. Animals were acclimated to holding conditions for a minimum period of 1 month prior to starting tests. Except during feeding trials, muskrats were maintained on a diet of lab chow (Wayne F-6 Rodent Blox, Teklad Premier Laboratory Diets, Madison, Wisconsin, USA) supplemented with apples and carrots. Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

We randomly tested each animal in 3 food consumption trials: a 24-hr D₂O trial, a 48-hr D₂O trial, and a 24-hr control trial (see below).

Muskrats were fed rhizomes of cattail during all trials and were fasted overnight to ensure they ate during the testing periods. Fresh rhizomes collected from Oak Hammock Marsh were fed to muskrats tested in September and October. For trials completed during November and December, muskrats were fed rhizomes collected prior to freeze-up and stored in peat moss at 5°C (Campbell and MacArthur 1996). During each trial, the muskrat resided in a 183- × 175- × 72-cm tank installed in a controlled-environment room (MacArthur and Campbell 1994). This diving tank was filled to a depth of 65 cm with water at 17.0 ± 2°C. A wire screen mounted on a frame slightly below water level prevented muskrats from escaping and ensured complete submersion of the rhizome rations. This set-up forced muskrats to forage underwater, as they often do in nature, and ensured that normal quantities of surface water adhered to the vegetation recovered by foraging animals. Muskrats were able to surface in a 20.5-L Plexiglass chamber containing a dry, wooden resting platform. Prior to testing, all muskrats underwent an 8-hr training-run to familiarize them with the tank.

Following an overnight fast, each animal was weighed, lightly anesthetized with Halothane (MTC Pharmaceuticals, Cambridge, Ontario, Canada), and administered a preweighed intraperitoneal injection of D₂O (99.9% purity; ICN Biochemicals, Cleveland, Ohio, USA) at a dosage of 3 g/kg body mass. The dosage was measured to the nearest 0.1 mg by weighing the D₂O injection syringe before and after ejection. After a 3-hr equilibration period, the animal was again anesthetized, weighed, and a 3-mL blood sample obtained by cardiac puncture. This step was performed to estimate the animal's TBW content and to obtain the initial serum concentration of D₂O. Following recovery from anesthesia (approx 0.5 hr), the animal was transferred to the diving tank, which contained a preweighed ration of cattail rhizomes, and it remained there for 24 or 48 hr. Upon removal from the tank, the muskrat was again anesthetized, weighed, and a 3-mL blood sample taken as before. At the end of each trial, all uneaten rations were removed from the tank, weighed, and dried to constant mass in a drying oven at 73 ± 1°C. To estimate the dry mass of rhizomes offered to the animal, we determined the water content of a representative sample of each rhizome ration. The DMI was calculated as the

difference in dry mass between the rations offered and the uneaten rations remaining. We compared known rates of food intake to those derived from water-flux estimates using the D₂O dilution technique. The protocol for the control trials was identical to the 24-hr D₂O trials, except that animals were not anesthetized or injected with D₂O, and no blood samples were collected. The control trials were conducted to determine what effects, if any, the above procedures had on the level of forage intake.

Upon completion of all feeding trials, tests were conducted to verify that 3 hr was sufficient time for D₂O equilibration in body fluids. For this purpose, 6 muskrats were injected with 1 g D₂O/kg body mass and blood samples were drawn by cardiac puncture at regular intervals from 0.5 to 6.0 hr postinjection.

Blood samples were allowed to clot at 4°C, centrifuged, and the serum removed and stored at -20°C. Whenever possible, we collected urine samples voided at the times of the first and second blood samples. We distilled serum and urine samples by vacuum sublimation using an apparatus modeled after Stansell and Mojica (1968). The percent transmittance of the purified-water distillate was measured at 2,510.0/cm with a Model 881, Perkin-Elmer dual-beam infrared spectrophotometer and standard calcium-fluoride cells. The D₂O concentration of each sample was determined from a calibration curve that accounted for background levels of D₂O in body fluids (Campbell 1997).

Field Trials

Fifty-eight muskrats were livetrapped at Oak Hammock Marsh, injected with D₂O, and released. Recapture success was 45%, which provided 33 estimates of water flux from 27 animals during 5 sampling periods: 12–15 July 1994 (5 M, 4 F), 13–28 September 1994 (5 M, 2 F), 6–15 December 1994 (6 M, 5 F), 20–24 February 1995 (2 M, 3 F), and 9–12 May 1995 (1 M). To evaluate the accuracy of the D₂O technique for estimating TBW, 15 additional animals were trapped and sacrificed after blood sampling, 3-hr postinjection. Carcasses were skinned, eviscerated, and freeze-dried to constant mass to determine their true TBW content (mL). We found that the D₂O technique overestimated the TBW content of muskrats by an average of $7.6 \pm 0.9\%$. Therefore, all estimates of TBW

Table 1. Values used to estimate the mean daily water influx and intake of vegetation, dry matter, and assimilated energy of captive and free-ranging muskrats, Oak Hammock Marsh, Manitoba, 1994–95.

	Dry matter content of forage (%)	Energy content of forage (kJ/g dry matter)	Metabolizable energy digestibility (%)
Validation trials	9.50–17.01	16.44	66.50 ^a
Field trials			
July	6.43	16.36	48.86 ^b
Sep	10.61	17.24	46.53 ^b
Dec–Feb	16.97	16.88	54.89 ^b
May	7.83	16.94	39.08 ^b

^a From Campbell and MacArthur (1994).

^b From Campbell and MacArthur (1996).

derived by this method were multiplied by a correction factor of 0.929.

During each sampling period, live traps were set twice daily, and captured muskrats were transported by canoe or covered sled to a nearby laboratory at the Institute for Wetland and Waterfowl Research, Oak Hammock Marsh Conservation Center. Here, muskrats were weighed, lightly anesthetized, and injected with D₂O as described above. Following injection, each animal was marked with monel ear tags and a subcutaneous microchip transponder (Avid Marketing, Norco, California, USA) was inserted near the base of the tail. We released tagged muskrats at their sites of capture, and an attempt was made to retrap them 48–72 hr later. Recaptured muskrats were weighed, anesthetized, and a second blood sample taken.

We determined the composition, DM, energy content, and digestibility coefficients of natural diets following the procedures of Campbell and MacArthur (1994, 1996).

Calculations

Because our calibration curve corrected for background deuterium levels, we calculated TBW from the initial dilution of D₂O using a modified equation of Peppard et al. (1993):

$$\begin{aligned} \text{TBW (mL)} &= \{[\text{D}_2\text{O injected (g)}] \\ &\div [\text{Serum D}_2\text{O concentration} \\ &(\text{g D}_2\text{O/g H}_2\text{O})]\} \cdot 0.929. \end{aligned}$$

We used equations provided in Nagy and Costa (1980) to calculate water efflux and influx based on the progressive dilution of D₂O in body fluids. Because animal mass varied during

every trial, the equations used were those derived for calculating water efflux (eq 4) and influx (eq 5) when TBW content increases or decreases linearly with time (Nagy and Costa 1980).

We calculated dry-matter intake from the equation of Shoemaker et al. (1976) for a non-drinking animal in steady state:

intake of dry matter

$$\begin{aligned} & (\text{g} \cdot \text{kg}^{-1} \text{ body mass} \cdot \text{day}^{-1}) \\ & = \{[\text{mL H}_2\text{O influx} \cdot \text{kg}^{-1} \\ & \quad \text{body mass} \cdot \text{day}^{-1}] \\ & \quad \div [\text{mL H}_2\text{O/g DM} \\ & \quad + (\text{ME coeff.} \cdot \text{kJ/g} \\ & \quad \text{DM} \cdot 0.030 \text{ mL H}_2\text{O/kJ ME})\}, \end{aligned}$$

where ME = metabolizable energy. The coefficients of ME and DM and the energy content of vegetation consumed by muskrats are presented in Table 1. We estimated metabolic water production by assuming a conversion factor of 0.030 mL H₂O/kJ ME (Schmidt-Nielsen 1983). We determined the amount of fresh vegetation consumed by muskrats by dividing DMI by the DM content of the diet in each test period. Seasonal estimates of the daily intake of AE (kJ/kg^{0.75}) were derived from equation 5 of Shoemaker et al. (1976).

Statistics

We evaluated differences in DMI for the control, 24-hr D₂O and 48-hr D₂O trials, and all seasonal comparisons with a 1-way analysis of variance (ANOVA) followed by Tukey's studentized test to compare individual means. The single observation collected in May was omitted from this analysis but was included in regression models. For the field trials, treatment effects were evaluated initially for differences due to season, sex, and sex × season with a 2-way ANOVA (SAS Institute 1990). Since no sex-related differences were apparent ($P > 0.05$), data for both sexes were pooled. Mean estimates of TBW and water influx obtained from blood and urine samples were compared with paired *t*-tests. Significance was set at the 5% level and means are presented ± standard error (SE).

RESULTS

Laboratory Validation Trials

The mean daily DMI was 21.5 ± 2.0 ($n = 6$) for the 24-hr D₂O trials, 24.1 ± 5.5 ($n = 7$) for

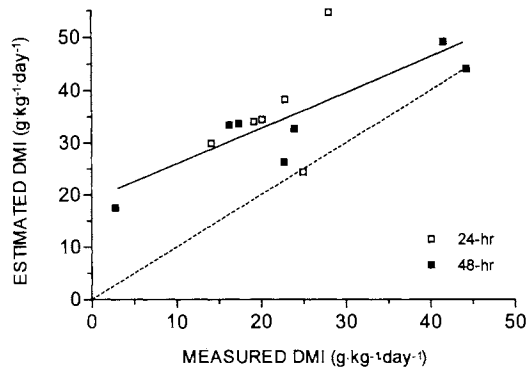


Fig. 1. Relation of dry-matter intake (DMI) estimated by the D₂O dilution method to measured DMI of lab-acclimated muskrats. The regression of estimated DMI on measured intake yielded the equation: estimated DMI = 19.36 + (0.68 × measured DMI); $r^2_{12} = 0.53$, $P = 0.005$. Values for the 24- and 48-hr trials were pooled for this analysis. The dashed line denotes equality between estimated and measured rates of food intake.

the 48-hr D₂O trials, and 30.3 ± 9.5 g/kg ($n = 7$) for the control trials ($F_{2,17} = 0.45$, $P = 0.65$). Thus, anesthesia and blood-sampling procedures did not appear to significantly reduce feeding levels of muskrats. The regression of estimated food intake on measured intake (Fig. 1) yielded the equation: estimated DMI = 19.36 + (0.68 × measured DMI), where $r^2_{12} = 0.53$, $P = 0.005$. Daily rates of water influx were highly variable, ranging from 97 to 430 mL·kg⁻¹·day⁻¹ ($\bar{x} = 243.5 \pm 24.0$). Over this range, DMI estimated from D₂O dilution exceeded measured intake by an average of 52.2%. However, as water influx and DMI increased, this error was substantially reduced (Fig. 1). For example, the error in estimating DMI was only +9.2% at a mean water influx of 349 mL·kg⁻¹·day⁻¹ (measured DMI > 40 g·kg⁻¹·day⁻¹), which is well below the minimal influx obtained under field conditions (see below).

Serial blood samples confirmed that D₂O had equilibrated with body fluids within 3 hr following D₂O injection. Values recorded as early as 30 min and as late as 300 min following injection of D₂O differed little from measurements recorded at 180 min postinjection.

We obtained urine samples at the time of blood collection (3 hr post-D₂O injection) on 7 occasions ($n = 6$ muskrats). Total body water estimated from these urine samples ($\bar{x} = 433.2 \pm 39.2$ mL) was nearly identical ($t_6 = 0.29$, $P = 0.78$) to that derived from serum analysis ($\bar{x} = 431.8 \pm 41.6$ mL), indicating that D₂O had equilibrated in both urine and plasma fluid compartments. Estimates of daily rates of water

influx based on analysis of urine samples ($\bar{x} = 198.5 \pm 48.3$ mL $\text{H}_2\text{O}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$) were similar ($t_3 = 0.14$, $P = 0.89$) to those derived from serum measurements ($\bar{x} = 200.6 \pm 45.2$ mL $\text{H}_2\text{O}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$).

Field Trials

In all but 3 cases, muskrats lost body mass over the 48–72-hr measurement interval (Table 2). However, mass loss was not different among months ($F_{3,28} = 1.51$, $P = 0.23$). Water influx varied seasonally ($F_{3,28} = 17.81$, $P < 0.001$), ranging from 423 to 915 mL $\text{H}_2\text{O}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$ (Table 2). The calculated intake of fresh vegetation also varied seasonally ($F_{3,28} = 14.19$, $P < 0.0001$), with the highest values recorded in spring and summer (Table 2). Interestingly, DMI ($\text{g}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$ and $\text{g}\cdot\text{kg}^{-0.75}\cdot\text{day}^{-1}$) peaked in December and February, when water influx and intake (wet mass) of fresh vegetation were lowest (Table 2). Similarly, the daily intake of AE ($\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{day}^{-1}$) was highest in winter ($P < 0.05$), when it was 62.6% greater than in July and 25.9% greater than in September. These trends are consistent with the reduced water content and higher ME digestibility of winter forage (Table 1). The DM content of forage (Table 1) proved to be a reasonable predictor of both daily water influx and intake of fresh vegetation: water influx ($\text{mL}\ \text{H}_2\text{O}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$) = $1,086.9 - (38.5 \times \%DM)$, where $r^2_{32} = 0.66$, $P < 0.0001$; vegetation intake ($\text{g}\ \text{wet mass}\cdot\text{kg}^{-1}\cdot\text{day}^{-1}$) = $1,123.8 - 37.0 \times \%DM$, where $r^2_{32} = 0.61$, $P < 0.0001$. Although no significant differences between sexes were detected for any of the variables measured, females tended to exhibit the highest intake of vegetation and AE within each sampling period.

DISCUSSION

Laboratory Validation Trials

Measured DMI of muskrats in D_2O trials (Fig. 1) averaged only 45–64% of values previously reported for captive animals consuming cattail rhizomes (Campbell and MacArthur 1994, 1996). It is unlikely that these low intake values were due to trauma associated with anesthesia or blood sampling procedures because control values were similarly low. However, Campbell (1997) previously observed that an abrupt shift in diet from lab chow to natural vegetation can markedly reduce forage intake of lab-acclimated muskrats, and we believe this phenomenon is responsible for the low DMI

Table 2. Seasonal changes in estimated daily water influx and intake of vegetation, dry matter, and assimilated energy of free-ranging muskrats, Oak Hammock Marsh, Manitoba, 1994–95.

Measurement	Jul (n = 9)		Sep (n = 7)		Dec (n = 11)		Feb (n = 5)		May (n = 1)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Body mass (g)	881A ^a	33	817AB	86	695B	43	686AB	48	825	48
Change in BM ^b (g)	-69	21	-42	13	-70	8	-34	15	-6	15
Water influx (mL·kg ⁻¹ BM·day ⁻¹)	841.0A	68.0	648.0B	63.7	444.0C	17.0	423.4C	45.3	914.6	45.3
Vegetation intake (g wet mass·kg ⁻¹ BM·day ⁻¹)	884.2A	71.5	704.8AB	69.3	506.0C	19.4	482.5BC	51.6	975.8	51.6
Dry matter intake (g·kg ⁻¹ BM·day ⁻¹)	56.9B	4.6	74.8A	7.4	85.9A	3.3	81.9A	8.8	76.4	8.8
Dry matter intake (g·kg ^{-0.75} BM·day ⁻¹)	54.9B	2.8	70.6AB	7.4	78.1A	3.1	74.4AB	7.9	72.8	7.9
Assimilated energy (kJ·kg ^{-0.75} BM·day ⁻¹)	438.6C	33.8	566.2BC	59.6	724.0A	28.6	689.1AB	73.3	482.0	73.3

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

^b BM = body mass.

observed in these trials. Earlier studies involved either acclimated animals that were held for 5 days on the rhizome diet prior to testing (Campbell and MacArthur 1994) or recently caught muskrats that were maintained on natural diets throughout their stay in captivity (Campbell and MacArthur 1996).

The D₂O dilution method overestimated DMI in most cases. This error may have arisen from 2 sources. First, as muskrats could breathe only in a Plexiglass chamber that contained saturated air, significant quantities of unlabeled water may have entered the body water pool via the lungs (Nagy and Costa 1980). A second potential source of error is the ingestion of unlabeled water from sources other than preformed water in the food. Previous digestion trials (Campbell and MacArthur 1994, 1996; Campbell 1997) indicated that muskrats can obtain sufficient moisture from preformed water in their food. However, at very low feeding rates, muskrats may be forced to drink small amounts of water to remain hydrated. Thus, an increased dependence on drinking water with declining DMI could account for the high discrepancy between estimated and measured DMI at low intake levels (Fig. 1). However, with increased water influx, even at levels less than those observed in field trials (Table 2), the D₂O technique provides a reasonably accurate estimate of DMI.

Field Trials

Rodents often lose mass with repeated captures (Kaufman and Kaufman 1994). On average, muskrats lost 7.4% of body mass between the first and second captures, which is equivalent to approximately 50% of a typical gut fill (Campbell 1997). Nonetheless, monthly estimates of DMI and AE obtained by the D₂O method (54.9–78.1 g·kg^{-0.75}·day⁻¹ and 438.6–724.0 kJ·kg^{-0.75}·day⁻¹) were nearly identical (2-sample *t*-tests: $t_{13-16} = 0.24-1.59$, $P = 0.13-0.81$) to those derived from total-balance digestion trials (59.7–75.9 g·kg^{-0.75}·day⁻¹ and 406.0–706.9 kJ·kg^{-0.75}·day⁻¹) involving field-acclimated muskrats (Campbell and MacArthur 1996). Results of both studies indicate that free-ranging muskrats increase their intake of DM and AE during fall and winter and are consistent with the finding that muskrats maintain the largest amount of gut tissue during these periods (Virgl and Messier 1992, Campbell and MacArthur 1996). An increased intake of forage

combined with enhanced energy and nutrient digestibility during these seasons (Campbell and MacArthur 1996) may also account for the substantial fat accumulation beginning in fall and continuing throughout winter (Virgl and Messier 1992, Campbell 1997).

In winter, cattail rhizomes have a high DM content (Table 1), are rich in energy and soluble carbohydrates, and are highly digestible (Campbell and MacArthur 1996). Consumption of a diet consisting primarily of cattail rhizomes apparently allows muskrats to increase intake of DM and AE while actually reducing gross intake of wet vegetation. Because individual tubers can attain a mass of several hundred grams (Campbell 1997), it is possible that muskrats in winter can meet their maintenance energy requirements with fewer daily excursions than in summer, when they feed predominately on the basal stems of emergent plants. This winter diet may be adaptive, given that the low water temperature and translocation of nutrients from plant shoots to underground root structures should, in theory, increase the energetic cost of aquatic foraging in this species.

Cattail is a preferred food of muskrats (Pelikán et al. 1970, Lacki et al. 1990), and cattail stands are favored locations for construction of winter lodges (Clark 1994). Moreover, muskrats overwintering in stands of cattail exhibited the highest survival rates and greatest gains in body mass (Clark and Kroeker 1993, Clark 1994). These observations are consistent with our previous findings (Campbell and MacArthur 1994, 1996) that coefficients of DM and ME digestibility are highest on diets of cattail rhizomes.

MANAGEMENT IMPLICATIONS

The results of this study indicate that the D₂O technique provides a valid method for assessing food consumption of free-ranging muskrats. Our results also demonstrate that reliable estimates of TBW and water influx can be achieved from analyses of urine voided by muskrats following D₂O injection. Muskrats tend to urinate upon handling; hence, the potential trauma associated with anesthesia and blood sampling can be avoided if an appropriate system is devised to collect voided urine.

Our field trials indicate that muskrats consume 750–1,000 g of fresh vegetation per kilogram of body mass each day from spring until late fall. This estimate is slightly above the daily spring and fall food requirement (734 g/kg of

body mass) reported by Ching and Chih-Tang (1965) for muskrats held in outdoor enclosures but is lower than the average daily intake of 1,250 g/kg (range = 875–1,800 g/kg) reported by Akkermann (1975) for captive muskrats in summer. Our field estimate of winter food consumption (550–600 g vegetation·kg⁻¹ body mass·day⁻¹) is close to the mean intake (513 g·kg⁻¹·day⁻¹) of captive, winter-acclimatized muskrats fed cattail rhizomes (Campbell and MacArthur 1996). However, it is well below the 1,200 g·kg⁻¹·day⁻¹ reported by Akkermann (1975) for captive muskrats fed a diet of cattail rhizomes in winter.

This study provides a first essential step in quantifying the forage requirements and energy exchange of free-ranging muskrats. Since muskrats can digest several emergent plant species equally well (Campbell and MacArthur 1994), our seasonal values for intake of DM and AE (Table 2) can be used to estimate the consumption of vegetation by muskrats occupying a wide range of emergent plant communities. When combined with reliable estimates of the amount of vegetation wasted or used in house construction, these data can be used to assess the effect of muskrats on the primary productivity of a variety of wetland habitats.

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EFFECT OF WINTER TEMPERATURE ON WILD TURKEY METABOLISM

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Abstract: We used indirect calorimetry to measure the effects of air temperature (T_a), age class, and body mass on metabolic rates of 9 adult and 7 juvenile female eastern wild turkeys (*Meleagris gallopavo silvestris*) during winter. Previous studies produced disparate results on this important aspect of winter ecology of wild turkeys. Standard metabolic rates (SMRs) of adult and juvenile hens were not different ($P = 0.122$) and averaged 28.69 mL $O_2 \cdot \text{min}^{-1} \cdot \text{bird}^{-1}$. Wild turkey metabolism increased with decreasing T_a ($P < 0.001$) below the lower critical temperature (T_{lc}) of 10.9°C. Metabolic rates were not related to body mass ($P = 0.571$), and age-specific metabolic rates were not distinguishable ($P = 0.998$). We estimated that a flock of 20 hens would need to find 400 g/day of additional food to meet thermoregulatory demands for each 10°C drop in T_a below 10.9°C.

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Malnutrition and starvation threaten northern populations of wild turkeys during winters with deep snow and cold temperatures (Austin and DeGraff 1975, Wunz and Hayden 1975, Porter et al. 1980). Schorger (1942) reported that the northern extent of wild turkey distribution in Wisconsin during the 1800s retreated south in severe winters and expanded north fol-

lowing mild winters. Since 1980, wildlife managers in the northern United States have transplanted wild turkeys north of their historic range (Kennamer and Kennamer 1990). Hence, information on the tolerance of wild turkeys for cold weather is needed to guide management decisions relative to wild turkeys at the northern edge of their range and beyond.

Effects of cold weather on energy requirements of wild turkeys may be predicted from measurements of the association between metabolic rate, T_a , and T_{lc} . Gray and Prince (1988)

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