Heat increment of feeding and its thermoregulatory benefit in the muskrat (*Ondatra zibethicus*)

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Abstract. The calorigenic effect of feeding and its potential benefit in defraying thermoregulatory costs and attenuating immersion hypothermia of adult muskrats were investigated. A single session of feeding on aquatic vegetation was sufficient to raise the metabolic rate of muskrats for a period of at least 5 h. The peak postprandial rate of oxygen consumption averaged 1.42 times the level established for fasted animals, and the heat increment of feeding accounted for about 40% of the metabolizable energy intake of muskrats. There was no evidence of a postprandial rise in oxygen consumption of muskrats that entered water at 18–19 °C after feeding. In aquatic trials, average and minimum steady-state oxygen consumption rates of fed muskrats were similar to, or even lower than values recorded from fasted animals, implying substitution of heat increment of feeding for thermoregulatory heat production. Our data did not support the hypothesis that heat increment of feeding retards body cooling in water. Net body temperature decline in water was actually higher in fed animals than in fasted controls. However, since previously fed muskrats also entered water at an elevated body temperature, the final body temperature (at 30 min immersion) was similar in all groups. These findings suggest that metabolic heat generated incidental to preimmersion feeding could provide a thermoregulatory benefit to muskrats by reducing the need for active thermogenesis in water.

Key words: Heat increment of feeding – Aquatic thermoregulation – Muskrat, *Ondatra zibethicus*

Introduction

Despite impressive adaptations for curbing heat loss and responding thermogenically to cold, many aquatic en-

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dotherms reveal only a modest capacity to thermoregulate in water (MacArthur 1989). Faced with the prospect of pending hypothermia, these animals should be expected to capitalize on heat produced incidental to other activities, including swimming and feeding (Costa and Kooyman 1984; Baudinette et al. 1986). They might exploit, for example, the HIF which comprises the additional heat produced in the mechanical processing, digestion, absorption, and metabolic transformations of assimilated nutrients (Blaxter 1989).

That HIF may substitute, at least in part, for cold-induced thermogenesis has been amply demonstrated in a variety of terrestrial endotherms (Simek 1976; Biebach 1984; Masman et al. 1988). The potential for HIF to defray thermoregulatory costs in water was first examined by Costa and Kooyman (1984) in a study of the sea otter, *Enhydra lutris*. These investigators reported a 54% rise in peak MR following feeding, and they proposed that these animals rely on HIF for maintaining thermal balance during long rest periods at sea. More recently, Baudinette et al. (1986) showed that the MR of the little penguin, *Eudyptula minor*, is nearly doubled following feeding, leading these authors to speculate that *E. minor* also may draw upon HIF to thermoregulate in water.

The possibility that other aquatic endotherms incorporate HIF into thermoregulatory tactics remains to be tested. An excellent model for investigating this problem is provided by the muskrat, *Ondatra zibethicus*. Holarctic in distribution, these amphibious rodents are surprisingly prone to immersion hypothermia (Hart 1962; MacArthur 1979a, 1984). Even brief episodes of swimming in cold water are sufficient to elicit pronounced abdominal cooling and a threefold rise in MR of *O. zibethicus* (MacArthur 1984). Earlier studies have underscored the value of stored body heat to aquatic endurance in muskrats, and revealed the extent to which these rodents depend upon behavioral mechanism to regulate T_b in nature (MacArthur 1979a, 1984). However, it is conceivable that muskrats might also utilize HIF to attenuate, if not avoid, immersion hypothermia. This is especially

true in winter, when muskrats feed intermittently throughout the day. During this season, muskrats may average 8–9 foraging trips per 24-h period, each lasting 20–250 min (MacArthur 1980). It is thus possible that HIF may persist over successive activity bouts in these northern rodents.

The objectives of this study were twofold: first, we wished to estimate the magnitude and approximate duration of HIF in muskrats fed the aquatic vegetation which constitutes their normal diet. To date, almost all studies of HIF in aquatic mammals have dealt with strictly carnivorous species (Gallivan and Ronald 1981; Costa and Kooyman 1984). A second goal was to test the hypothesis that HIF attenuates body cooling and substitutes partially or completely for thermoregulatory heat production in water. This hypothesis predicts that recently fed muskrats should cool less than fasted animals in water, and that differences in MR between fed and fasted animals should be reduced in the aquatic environment. If fed muskrats are more resistant to aquatic cooling, we also predicted that they should engage in more exploratory dives than fasted animals. Since the act of eating involves muscular work which generates substantial heat in at least some mammals (Gallivan and Best 1986; Blaxter 1989), we also determined if feeding in water benefits aquatic thermoregulation in the muskrat.

Materials and methods

Animals. A total of ten adult muskrats (eight females, two males) ranging in mass from 757 to 1107 g were used in this study. Muskrats were livetrapped in Oak Hammock marsh near Winnipeg, Manitoba (50°06'N; 98°20'W) in early May and transported to the Department of Zoology, University of Manitoba. Animals were maintained on an ad libitum diet of commercial rodent chow (Agway Prolab) supplemented by apples and carrots. Details concerning laboratory holding facilities are provided elsewhere (MacArthur 1979b; 1984). Muskrats were acclimated to holding conditions for a minimum period of 1 month prior to beginning tests, which were conducted during June and July, 1990 and 1991.

Body temperature measurements. Abdominal T_b was recorded from each animal using a 1.5-g model X-M transmitter (mini-Mitters Inc., Sunriver, Ore., USA) surgically implanted into the abdominal cavity. Transmitter calibration and implantation procedures followed MacArthur (1979b) and Dyck and MacArthur (1992). Transmitter signals were detected with a Sony AM receiver. All surgery was completed at least 2 weeks prior to starting experiments.

Heat increment of feeding. The thermogenic response to ingested forage was estimated by monitoring the increase in RMR after a single, 70-min session of feeding. Following a 22-h fast, each muskrat was provided with 270–300 g (wet mass) of a standardized ration consisting of the stems of sedge (*Carex atherodes*) and bulrush (*Scirpus lacustris*), and the stems, roots and rhizomes of cattail (*Typha glauca*). These emergent species all constitute natural forages of the muskrat in northern prairie marshes. Vegetation was collected from local marshes, including Oak Hammock, usually on the day preceding a given feeding trial.

Prior to feeding, rations were thoroughly washed, blotted dry, and weighed to within 0.1 g. Food was placed in the muskrat's holding cage at 0800 hours and feeding was permitted until 0910 hours, when the animal was removed and immediately installed

in the metabolic chamber (see below). An average of 12 min elapsed between the end of feeding and the initiation of metabolic measurements. To estimate dry matter intake in each trial, a duplicate ration sample was prepared, weighed, dried to constant mass at 70 °C, and reweighed. The dry:wet mass ratio derived for this sample was used to calculate dry matter content of the forage ration. This value, less the dry mass of uneaten rations, provided an estimate of dry matter intake.

For each trial, the dried ration sample and uneaten rations were ground separately in a Wiley mill. The gross energy content of each was determined in triplicate using an adiabatic O_2 bomb calorimeter (Parr 1241 Calorimeter, Parr Instrument Co., Moline, Ill., USA). On a dry matter basis, the rations fed to muskrats contained, on average, 7.9% protein, 12.5% ash, and 61.9% neutral detergent fiber (feed analysis laboratory, Department of Animal Science, University of Manitoba). The mean ($\pm$SEM) gross energy content of the forage ration was 16.41 ± 0.25 kJ·g^{-1} dry matter.

All metabolic measurements in air were made at thermoneutrality (15 ± 0.5 °C). The respirometry chamber consisted of a darkened, 14-l glass box fitted with a heavy Plexiglas lid and a removable Plexiglas floor. A positive-pressure, open-circuit system similar to that described by MacArthur (1984) was used, in which inlet flow rate was maintained at 4.5 l·min^{-1} with a Matheson rotameter calibrated against a model 1057 Brooks Vol-U-Meter. Exhaust gas from the chamber was split into two streams. One stream was routed through drierite followed by soda lime/drierite, and then through a S3-A oxygen analyzer (Applied Electrochemistry Inc.) connected to a two-channel chart recorder (SE-120, BBC Goerz Metrawatt). The second exhaust stream was routed through drierite and then through a CD-3A carbon dioxide analyzer (Applied Electrochemistry Inc.) connected to the second channel of the recorder. Minimum steady-state rates of O_2 consumption and CO_2 production were calculated for successive 0.5-h intervals (Wang and Peter 1975). The respiratory quotient derived from these measurements was used to convert $\dot{V}O_2$ values to units of heat production, W·kg^{-1} (Stanier et al. 1984).

MR was monitored for 7.5 h following ingestion of the meal. Control runs of similar duration were also performed on each animal in a fasted state, following 22 h food deprivation. Only one feeding and one control trial were performed per animal, with the order of the trials randomized. Since adequate resting values were not obtained for two of the muskrats tested, data for these individuals were omitted from the analyses.

Aquatic trials. Aquatic tests were performed in a fibreglass-lined, plywood tank ($183 \times 175 \times 72$ cm) housed in a controlled-environment room. The tank was filled to a depth of 68 cm with water at 18.5 ± 0.5 °C. Wire screen covers secured to a frame 3 cm below water level prevented diving muskrats from surfacing at any point in the tank other than the metabolic chamber. The latter consisted of a 20.5-l Plexiglas box fastened to the submerged frame (MacArthur and Krause 1989). Exhaust gas from the chamber was drawn by vacuum through drierite and soda lime/drierite trains and then through a calibrated Matheson rotameter at a rate of 10.5 l·min^{-1}. Otherwise, the respiratory set-up and the method for calculating average $\dot{V}O_2$ in water were identical to those described by MacArthur and Krause (1989). When possible, minimum steady-state $\dot{V}O_2$ in water was also calculated, using Eq. 4a of Withers (1977). In these instances, muskrats typically floated quietly in the chamber and only occasionally engaged in short exploratory dives. Abdominal T_b was recorded at 5-min intervals throughout each 30 min immersion period. The frequency and duration of all voluntary dives were also noted.

Muskrats were tested under four experimental situations. Trial A provided a control in which muskrats were fasted for 22 h and received no food either before or during immersion. In Trial B, fasted muskrats were provided with a natural forage ration identical to that described for the HIF experiment (see above). In this case, animals were permitted to feed for 70 min prior to entering water, but not during immersion. Trial C involved muskrats that

were not fasted, but were maintained on the standard laboratory diet of rodent chow supplemented by apples and carrots. To ensure that they had recently fed, animals in this trial were provided additional apples and carrots 70 min before release into the tank. Trial D involved fasted muskrats that were fed only in the water. In this case, the stems and rhizomes of sedge, cattail and bulrush were placed beneath the screen cover of the tank, close to the metabolic chamber. Muskrats could thus "forage" in the tank and consume vegetation they collected while floating in the chamber. Trial D was the only experiment in which muskrats could feed during metabolic measurements. Trial order was randomized and at least 72 h separated successive tests on the same individual. Each animal was tested twice in a given trial.

Statistical treatment of data. Means were compared with Student's *t*-test or, for multiple comparisons, analysis of variance (GLM procedure, Statistical Analysis System, Cary, N.C., USA) and Fisher's LSD test. Significance was set at the 5% level and means are presented ±1 SEM.

Results

Heat increment of feeding

The gross energy intake of muskrats fed aquatic emergent vegetation prior to HIF determinations averaged 75.9 ± 19.3 kJ. This is approximately 12% of the daily gross energy intake of captive muskrats maintained on similar diets in the laboratory (K.L. Campbell and R.A. MacArthur, unpublished data). Ingestion of the single meal by muskrats was followed by a rise in RMR that persisted throughout the 7.5-h postprandial measurement period (Fig. 1). However, differences in mean $\dot{V}O_2$ between fed and fasted animals were not significant beyond 5 h ($P > 0.05$), suggesting that the major thermogenic response to feeding was completed within 5 h of ingesting the meal. The $\dot{V}O_2$ of fasted muskrats did not change significantly during the test session (Fig. 1).

During the first 5 h following feeding, mean postprandial $\dot{V}O_2$ (0.99 ± 0.06 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) was 1.24 times the mean postabsorptive value (0.80 ± 0.02 ml $O_2 \cdot g^{-1} \cdot h^{-1}$). Peak postprandial RMR averaged $1.14 \pm$

0.07 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ or 1.42 times the control level. Based on the calculated difference in heat production of fed and fasted muskrats (Fig. 1), the estimated HIF was 16.9 kJ. Assuming an apparent metabolizable energy coefficient of 0.531 (K.L. Campbell and R.A. MacArthur, unpublished data), this heat increment would account for 42% of the metabolizable energy (40.3 kJ) ingested by muskrats.

For the first 30 min of testing, the mean T_b of postprandial muskrats (38.0 ± 0.09 °C) exceeded that of controls (37.2 ± 0.29 °C; $t = 2.61$, $df = 14$, $P < 0.03$). Thereafter, T_b was similar in both groups (Fig. 1, $P > 0.05$).

Feeding and aquatic thermoregulation

Contrary to expectations, net T_b decline in water was greatest in muskrats that had fed prior to immersion (Trials B and C; Table 1, Fig. 2). The initial (preimmersion) T_b of recently fed animals (Trials B and C) also averaged 1.0–1.2 °C higher than for animals that were fasted prior to release into the water (Trials A and D, Fig. 2). However, owing to the higher cooling rates of postprandial muskrats, mean T_b was similar for all test groups after 30 min in water (Table 1, $P > 0.05$). Abdominal cooling was least pronounced in muskrats that were permitted to feed on aquatic vegetation during the test session (Trial D, Table 1). In all aquatic trials, the net decline in T_b was positively correlated with cumulative dive time (Fig. 3).

There was no evidence of a postprandial rise in $\dot{V}O_2$ of muskrats that entered water after feeding. In fact, the lowest average $\dot{V}O_2$ in water (1.70 ± 0.06 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) was recorded for animals fed prior to immersion (Trial B, Table 1). The highest average $\dot{V}O_2$ in water (2.24 ± 0.05 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) was recorded for Trial D when muskrats could forage underwater and feed in the respirometry chamber. For the remaining trials, minimum steady-state $\dot{V}O_2$ in water was similar ($P > 0.05$), ranging from 1.26 ± 0.06 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ in Trial B, to 1.35 ± 0.06 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ in Trial A.
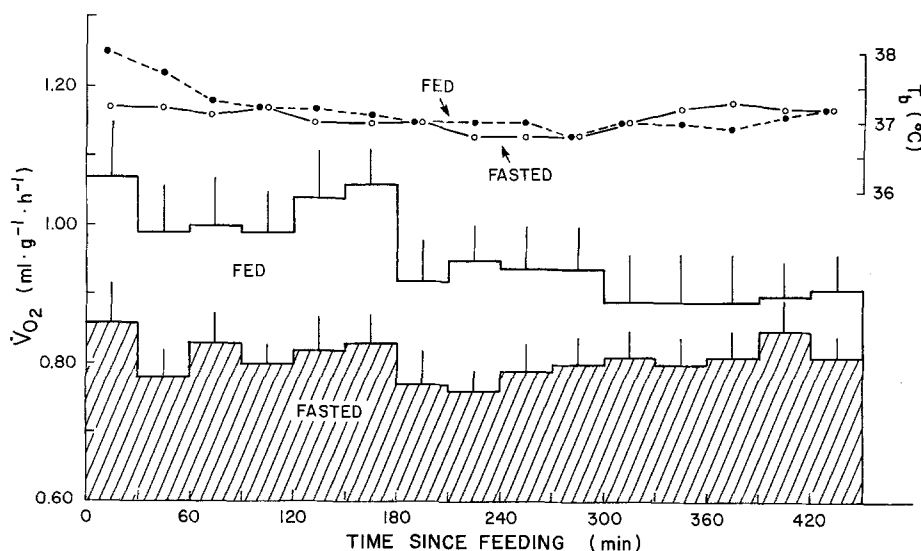
Fig. 1. Mean $\dot{V}O_2$ and telemetered body temperatures (T_b) of muskrats ($n = 8$) after a single session of feeding on aquatic vegetation (*open bars*, ●), and in postabsorptive state following a 22-h fast (*hatched bars*, ○). *Vertical bars* denote 1 SEM
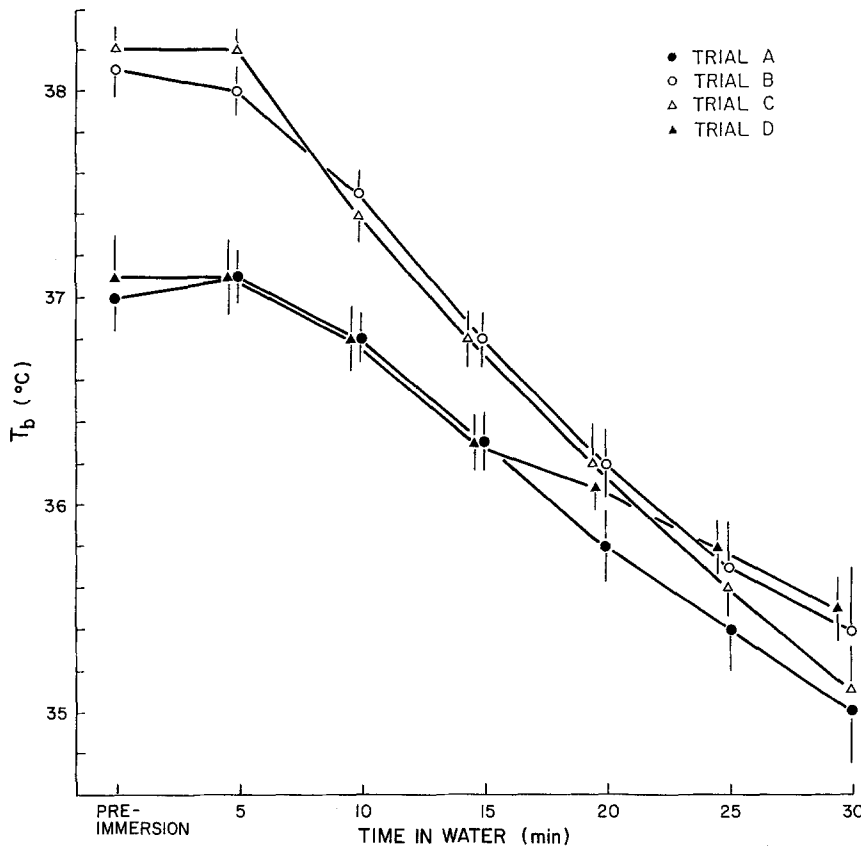
Fig. 2. Temporal variation in mean ($\pm$SEM) body temperature (T_b) of unrestrained muskrats ($n=10$) during 30 min of immersion in water at $18.5\pm0.5\,°C$ (Trials A–D)

Table 1. Summary of diving, average $\dot{V}O_2$, and body temperature responses of unrestrained muskrats ($n=10$) to 30 min of immersion in water at $18.5\pm0.5\,°C$

Trial	Cumulative dive time per 30-min run (s)	No. of dives per 30-min run	Dive duration (s)	Average $\dot{V}O_2$ in water ($ml\cdot g^{-1}\cdot h^{-1}$)	Body temperature (°C)		
					Pre-immersion	Final in water (30 min)	Net change
A	$607.8^a\pm45.3$	$21.4^{a,b}\pm1.88$	$29.9^a\pm1.69$	$1.91^b\pm0.05$	$37.0^b\pm0.16$	$35.0^a\pm0.25$	$2.0^{b,c}\pm0.24$
B	$602.0^a\pm65.8$	$19.0^{b,c}\pm1.89$	$32.0^a\pm2.12$	$1.70^c\pm0.06$	$38.1^a\pm0.13$	$35.4^a\pm0.29$	$2.7^{a,b}\pm0.28$
C	$704.8^a\pm52.6$	$25.1^a\pm1.77$	$28.3^a\pm1.29$	$2.01^b\pm0.08$	$38.2^a\pm0.12$	$35.1^a\pm0.27$	$3.1^a\pm0.25$
D	409.1 ± 24.9	$15.2^c\pm1.01$	$28.0^a\pm1.66$	$2.24^a\pm0.05$	$37.1^b\pm0.21$	$35.5^a\pm0.15$	$1.6^c\pm0.21$

Aquatic tests were performed on animals which were fasted only (Trial A), fed prior to, but not during immersion (Trials B and C), or fasted, but permitted to feed in water during measurements (Trial D; see text for details)

Values are means $\pm$ SEM. Within each column, means sharing the same letter are not significantly different ($P>0.05$)

Cumulative dive time was similar for all trials except D (Table 1). In the latter experiment, animals spent an average of only 22.7% (409 s) of each 30-min session diving, compared to 33.4–39.2% (607–705 s) for the remaining trials. The total number of dives per 30-min session was also lowest in Trial D (Table 1). Muskrats in Trial D spent most of each run floating in the respirometry chamber, consuming vegetation retrieved from the tank. The average duration of individual dives was similar for all experiments (Table 1).

Discussion

Results of this study indicate that a single feeding of emergent vegetation is sufficient to raise the RMR of muskrats for a period of at least 5 h. Since muskrats in winter feed intermittently throughout the day, often leaving their dens for periods exceeding 1 h (MacArthur 1980), the HIF response is of adequate duration to be of thermoregulatory benefit to foraging animals. Conceivably, HIF generated in a given feeding session could defray thermoregulatory costs during the same, as well as on subsequent foraging trips during this season.

At low temperatures, a diminution in the thermogenic response to feeding is usually assumed to indicate partial substitution of HIF for thermoregulatory metabolic costs (Simek 1976; Masman et al. 1988; Klaussen et al. 1989; Robbins 1993). If this assumption applies also to muskrats in water, then our results strongly suggest that HIF offsets energy expended for aquatic thermoregulation. In no case did we detect a postprandial rise in
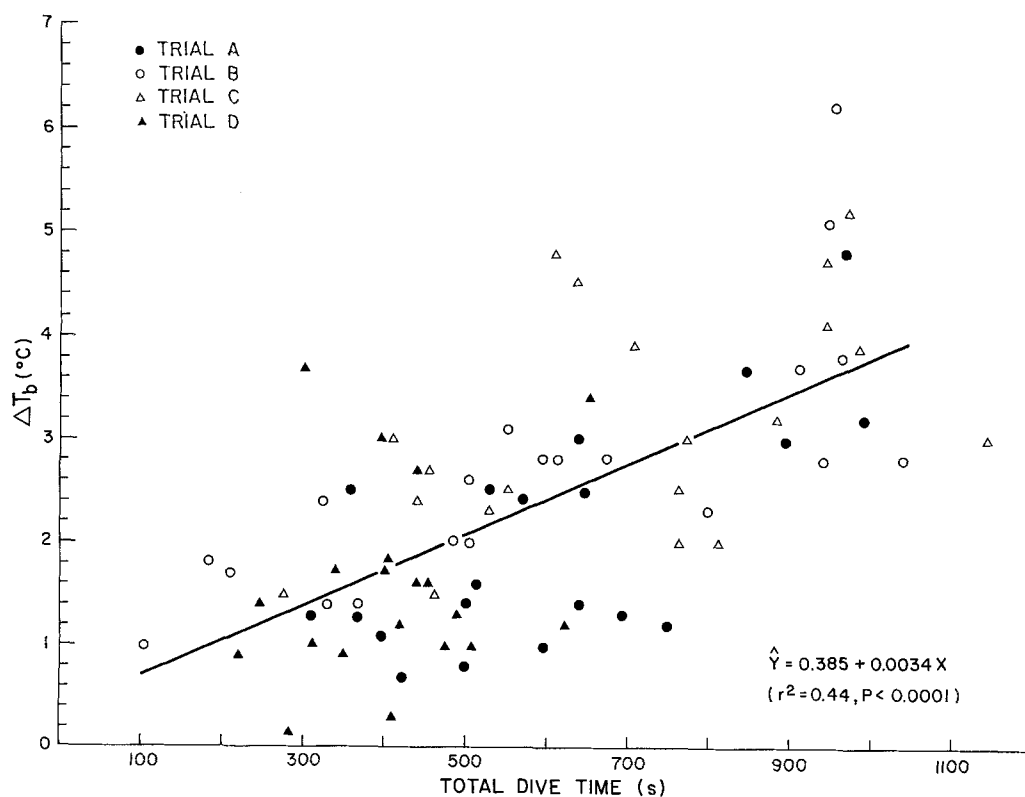
Fig. 3. The relationship between net body temperature change (ΔT_b) and cumulative dive time of unrestrained muskrats ($n=10$) immersed for 30 min in water at 18.5 ± 0.5 °C (Trials A–D). ΔT_b = final T_b in water − preimmersion T_b

the $\dot{V}O_2$ of immersed animals. The $\dot{V}O_2$ of muskrats permitted to feed immediately prior to entry into water (Trial B) was actually less than that of fasted controls (Trial A) despite similar dive times (Table 1).

Implicit in the argument that HIF substitutes for cold thermogenesis is the assumption that digestion and nutrient assimilation persist in the cold-challenged animal. In the case of a semiaquatic mammal like the muskrat, this tenet may be invalid if the animal vasoconstricts abdominal tissues in water, thereby suspending nutrient digestion and absorption. Thus, the apparent absence of a postprandial rise in $\dot{V}O_2$ of immersed muskrats might also indicate a temporary arrest in gut and liver functions associated with immersion. Further research involving regional blood flow measurements of muskrats in water is clearly needed to resolve this issue.

Interestingly, the only trial in which feeding appeared to influence the $\dot{V}O_2$ of immersed muskrats was Trial D, in which animals were permitted to feed while floating in the respirometry chamber. The 17% increase in $\dot{V}O_2$ of these animals is attributed to the muscular work required in the handling, mastication, and ingestion of aquatic plants. It is noteworthy that the $\dot{V}O_2$ of animals in Trial D increased relative to controls, despite a reduction in cumulative dive time (Table 1).

We found no evidence that HIF retards body cooling in water. In fact, net T_b decline was higher in fed animals than in fasted controls, implying a greater loss of body heat to the surrounding medium following ingestion of food. However, because previously fed muskrats also entered water at an elevated T_b, the final T_b (at 30 min immersion) was similar for all groups (Table 1). Thus,

one potential thermoregulatory benefit of preimmersion feeding in muskrats may be the incidental storage of metabolic heat that could reduce the need for active thermogenesis in water.

This heat storage benefit might explain, for example, why mean $\dot{V}O_2$ was 11% lower for fed muskrats in Trial B than for fasted animals in Trial A (Table 1). Although fed muskrats in Trial C did not demonstrate a reduction in MR, animals in this group also tended to do more diving than controls (Table 1). Consequently, increased motor costs associated with underwater swimming (MacArthur and Krause 1989) could have masked any thermoregulatory saving accrued from preimmersion heat storage in Trial C animals. Based on HIF trials (Fig. 1), the postprandial rise in T_b associated with a single session of feeding appears to be relatively short-lived, since it did not persist beyond about 30 min.

The only case in which we found evidence of attenuated body cooling in water was Trial D. While muscular heat generated secondarily to feeding might have contributed to the reduced T_b drop of muskrats in Trial D, a more important factor was probably the reduction in cumulative dive time of these animals (Table 1). As revealed in Fig. 3, net T_b decline increases with cumulative dive time in muskrats, an observation we attribute to the enhanced convective heat loss associated with whole-body submersion (MacArthur 1984).

The results of our HIF trials concur with earlier studies indicating that the calorigenic effect of feeding often accounts for more than 30% of metabolizable energy in mammalian herbivores (Robbins 1993). In the case of *O. zibethicus*, this observation may in part reflect the

high fiber content of the animal's diet (Robbins 1993). To our knowledge, the only other study of HIF in a herbivorous aquatic mammal is an investigation of the Amazonian manatee, *Trichechus inunguis* by Gallivan and Best (1986). These investigators were unable to detect any postprandial rise in the $\dot{V}O_2$ of manatees following a single feeding of aquatic vegetation. Not surprisingly, the peak postprandial rise in $\dot{V}O_2$ of muskrats (42%) was less than the 54–100% increase previously reported for marine birds and mammals fed high-protein, animal tissue diets (Gallivan and Ronald 1981; Costa and Kooyman 1984; Baudinette et al. 1986).

Finally, Wilson and Culik (1991) have proposed that a considerable portion of the HIF response may, in fact, represent heat required to warm ingested food from ambient to core temperature. In our HIF trials, muskrats consumed an average of 61.3 g (wet mass) of aquatic vegetation with a mean water content of 90.2% and an initial temperature close to 14 °C. If it is assumed this vegetation had a specific heat equivalent to that of water $(4.187 \text{ kJ} \cdot \text{kg}^{-1} \cdot {}^{\circ}\text{C}^{-1})$, then only 5.9 kJ, or about 35% of HIF would be utilized to warm ingested food to core T_b. This calculation likely over-estimates the true contribution of HIF to warming food, since feeding in this study was initiated more than 1 h prior to starting metabolic measurements. However, the cost of warming ingested food in nature may be significant, especially during winter, when muskrats consume large quantities of submerged vegetation retrieved from near-freezing water. As Wilson and Culik (1991) point out, the metabolic costs of warming ingested food could be mitigated in species like the muskrat, by spreading the foraging effort over a longer period of the day. This aspect of the muskrat's winter ecology and foraging energetics clearly warrants further investigation.

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