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METABOLIC EFFECTS OF SWIMMING VELOCITY AND WATER TEMPERATURE IN THE MUSKRAT (*ONDATRA ZIBETHICUS*)

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Abstract—1. Metabolic rates, $\dot{V}_{O_2}$, were studied in four muskrats ***(Ondatra zibethicus)*** swimming in a water channel at velocities of 0.2 to **0.75** m/s in water at temperatures of **25** and 30°C.

2. At both water temperatures, $\dot{V}_{O_2}$ increased linearly with increasing swimming velocity. The $\dot{V}_{O_2}$ was higher for muskrats swimming in water at **25** than 30°C.

3. The metabolic performance of swimming appears to be influenced by the interaction of swimming velocity and water temperature.

INTRODUCTION

The energetics of locomotion have received considerable attention (Schmidt-Nielsen, 1972; Tucker, 1975), but metabolic measurements of swimming have been largely confined to fish (see review by Webb, 1975). In the case of mammals, the swimming energetics have been empirically investigated only in muskrats (Fish, 1982a), sea lions (Costello & Whittow, 1975; Kruse, 1975) and humans (Holmer, 1972; DiPrampero ***et** al.*, 1974). With the exception of humans (see review by Nadel, 1977) studies of mammalian swimming energetics have not been concerned with the interaction of swimming effort with ambient water temperature. Since water is at least 25 times more thermally conductive than air at the same temperature (Fish, 1979) and faster swimming speeds would necessitate increased convective heat loss, the metabolism would have to be adjusted for increased swimming effort and thermoregulatory need.

A study was undertaken to examine the aerobic energetics of swimming at various velocities in the muskrat *(Ondatra* zibethicus). Animals swam in water at temperatures both below and at thermoneutrality. The principle intent of this investigation was to examine differences in metabolic input due to the potential interaction of ambient water temperature and swimming effort.

MATERIALS AND METHODS

Experimental animals

Four male muskrats were live-trapped in Ingham County, Michigan during the summer of **1979.** The mean body mass of the muskrats was **614.8** g (range **521–746** g) over the test period. To avoid mortality due to captivity throughout the period of testing, the animals were kept outdoors in a large, concrete pond at the Limnology Research Laboratory on the campus of Michigan State University. The pond had a depth of approx 2 m, allowing unrestricted swimming and diving. Abundant aquatic vegetation, which grew in the pond, was readily consumed by the muskrats and used for bedding material. The diet was supplemented with apples. The pond was equipped with a platform above the water. Nest boxes were provided on the platform and were modified for the capture of single animals when needed for testing.

Water channel and metabolic chamber

Experiments on swimming were conducted in a recirculating water channel, based on a design by Vogel & Labarbera **(1978)** and described previously by Fish (1982a). A working section was provided in the channel in which a single muskrat was allowed to swim. The upstream end of the working section was bounded by a platic grid in conjunction with a 5 cm wide grid of plastic straws, both of which removed turbulence from the water flow. The downstream end of the working section was bounded with a low voltage electric grid which stimulated swimming by the muskrat. Wires attached to the grid ran along the floor of the working section to prevent the animal from standing on the floor to rest. The voltage was controlled with a Powerstat (Superior Electric Co.). All electricity was disconnected to the grid when the muskrat maintained steady swimming. During higher velocity trials, a removable wall was placed in the working section to constrict its cross-sectional area and thus increase the water velocity.

On the top of the working section was a Plexiglas metabolic chamber of the dimensions of **75.5** x 13.0 x **26.0** cm. Inlet and outlet air tubes entered through the walls of the chamber. At its base, the metabolic chamber had a Plexiglas apron which extended over the working section. When the water channel was filled, the apron was slightly submerged below the water surface. This prevented any air leakage, but had little effect on the water flow. The dimensions of the metabolic chamber were large enough for a single muskrat to swim against a constant current without interference.

Water velocity (U), which was equivalent to the relative swimming velocity of the muskrat, was controlled by a Mercury electric outboard moter (Model No. **10019)** situated in the return channel of the water channel. Power to the motor was provided by a **12V** storage battery connected to a **6 A** battery charger. Motor speed was related to water speed, determined by the time a drop of ink or neutrally bouyant particle traversed a given distance.

Muskrats were tested in water at **25** and **30°C** at velocities ranging from **0.2** to **0.75** m/s. The arrangement of test velocities for each muskrat was such that there was no apparent order. Each muskrat was forced to swim steadily at a given test velocity for a period of 10–30 min to obtain sufficient data. During the initial exposure to the apparatus, each muskrat learned to swim steadily and avoid the downstream electrified grid within 15 min. Data were only collected during subsequent trials when the muskrat was proficient in swimming against the current.

Oxygen consumption

Mass-specific oxygen consumption ($\dot{V}_{O_2}$), as a measure of metabolic rate, was monitored using an open-circuit system conforming to condition B of Hill (1972). The oxygen content of dry, CO_2-free air flowing out of the metabolic chamber was monitored with a Beckman C-2 paramagnetic oxgen analyzer. Ascarite (**A.** H. Thomas Co.) and Dierite (**W.** A. Hammond Co.) were contained in tubes downstream of the metabolic chamber to absorb CO_2 and water vapor, respectively, from the air flow. The rate of air flow into the metabolic chamber was measured with a calibrated Gilmont Model 1300 flowmeter. The flow rate into the chamber was approx 3.0–3.8 l/min for dry air at STP.

In order to obtain a realistic estimate of the energy expenditure of natural muskrat swimming, experimental animals were not fasted prior to testing in order to control for specific dynamic action. After the experimental animal was placed in the metabolic chamber, the muskrat was given 10–30 min to adjust to the apparatus and water temperature. During this period, the resting V_{O_2} was recorded for the animal. During measurement of the resting V_{O_2}, the animals floated quietly with approx 1/3 of the total body surface area above the water.

Diffusion of oxygen between the air flow and water could produce an error in the measured $\dot{V}_{O_2}$. To test for this, a gas of known composition (88% N_2, 12% O_2) was passed through the metabolic chamber with the water current at a given velocity. Any change in the gas composition was monitored with the oxygen analyzer over a 30 min period. An error of approx 1% of the actual value of oxygen in the gas was found at 0.7 and 0.75 m/s, probably due to the turbulence produced by the motor. Apparent metabolic rates at 0.7 and 0.75 m/s were adjusted to compensate for this factor.

RESULTS

The mean resting $\dot{V}_{O_2}$ in water at 25 and 30°C was 0.86 ± 0.04 ($n = 48$) and 0.77 ± 0.04 ($n = 48$) cc O_2/g/hr ± SE, respectively. The mean resting V_{O_2} at 25°C was found to be significantly higher ($P < 0.05$; $df = 3$) than the mean value for muskrats in water at 30°C by use of a paired t-test (Steele & Torre, 1960). This difference was consistent with previous reports, in that 30°C in water represented the lower critical temperature of muskrats below which the metabolism increases (Hart, 1962; Fish, 1979).

Muskrats swam similar to the description by Mizelle (1935). They normally swam at the water surface maintaining a slightly lordotic posture. The forelegs were held under the chin, while the hindfeet moved in a paddling mode by alternating strokes. The compressed tail was thrown into a series of lateral waves, similar to anguilliform locomotion of fish (Fish, 1982b).

The relationship between net (total–resting) $\dot{V}_{O_2}$ and swimming velocity, U, for muskrats in water at 25 and 30°C ambient temperature is illustrated in Fig. 1. At both temperatures, the net $\dot{V}_{O_2}$ increased linearly with increasing U. Equations for the regressions of total and net $\dot{V}_{O_2}$ and 25 and 30°C are listed in Table 1. The total and net $\dot{V}_{O_2}$ regressions were higher at 25°C than 30°C, except for net $\dot{V}_{O_2}$ values for muskrats swimming below 0.23 m/s (Fig. 1).

An analysis of variance (ANOVA) for a repeated measures, two-factor design (Bauning & Kintz, 1977) of the net $\dot{V}_{O_2}$ showed statistical significance for the treatments of temperature ($P < 0.1$), velocity ($P < 0.005$) and the temperature–velocity interaction ($P < 0.05$). The significant interaction indicated a departure from parallel for the net $\dot{V}_{O}$, for each temperature, so that the metabolic rate increased faster with increasing U at 25 than at 30°C. ANOVA of the total $\dot{V}_{O_2}$ showed significant results for the temperature ($P < 0.025$) and velocity ($P < 0.005$), but not the temperature-velocity interaction.

DISCUSSION

For the muskrat, a semi-aquatic, endothermic homeotherm, the energetic expenditure for swimming appears to be influenced by the ambient water temperature in conjunction with the amount of work performed.

Muskrats exhibited a significant difference in the $\dot{V}_{O_2}$ between water temperatures of 25 and 30°C over the range of swimming velocities. The maximum total V_{O_2}, calculated from the regression equations at a U of 0.75 m/s, was found to be 22% higher at 25°C than at ***30°C*** water temperature. Pasquis et *al.* (1970) found that acclimated white mice, white rats, golden hamsters and guinea-pigs had the highest values of V_{O_2} when swimming in water at a low temperature.

In humans, Nadel *et al.* (1974) found that the metabolic cost of swimming at different water speeds and temperatures was greatest at the lower water temperature tested of 18°C. The higher $\dot{V}_{O_2}$ with increasing swimming speed in humans at 18°C water temperature compared to 26 and 33°C was believed due to increased metabolism for thermoregulatory needs supplied by shivering (Nadel *et al.*, 1974).

Although 25°C in water is below thermoneutrality for the muskrat (Hart, 1962; Fish, 1979), shivering was not observed in the exercising animals. Muskrats swimming in the summer showed an elevation of body temperature believed due to the rise in metabolic heat production which is not compensated for by a decrease in thermal insulation (MacArthur, 1979).

The slopes for the regressions between $\dot{V}_{O_2}$ and U in the present study were higher for muskrats in water at 25 than at 30°C. These differences were likely due in part to the convective effect of the velocity of the medium. Gessamen (1972) found that for the snowy owl (*Nyctea scandiaca)* at any air temperature the metabolic rate was a function of the ambient air temperature and the square root of the wind velocity. A similar relationship has been found for other birds

Table 1. Regressions for metabolic rates of muskrats swimming at various velocities, U and in different water temperatures, T_a

Metabolic rate	T_a ("C)	Velocity range (m/s)	$\dot{V}_{O_2} = aU + b$ a	b
Total	25	0.2–0.75	2.82	+0.69
Net	25	0.2–0.75	3.12	–0.32
Total	**30**	0.2–0.75	2.14	+0.70
Net	30	0.2–0.75	2.22	–0.11

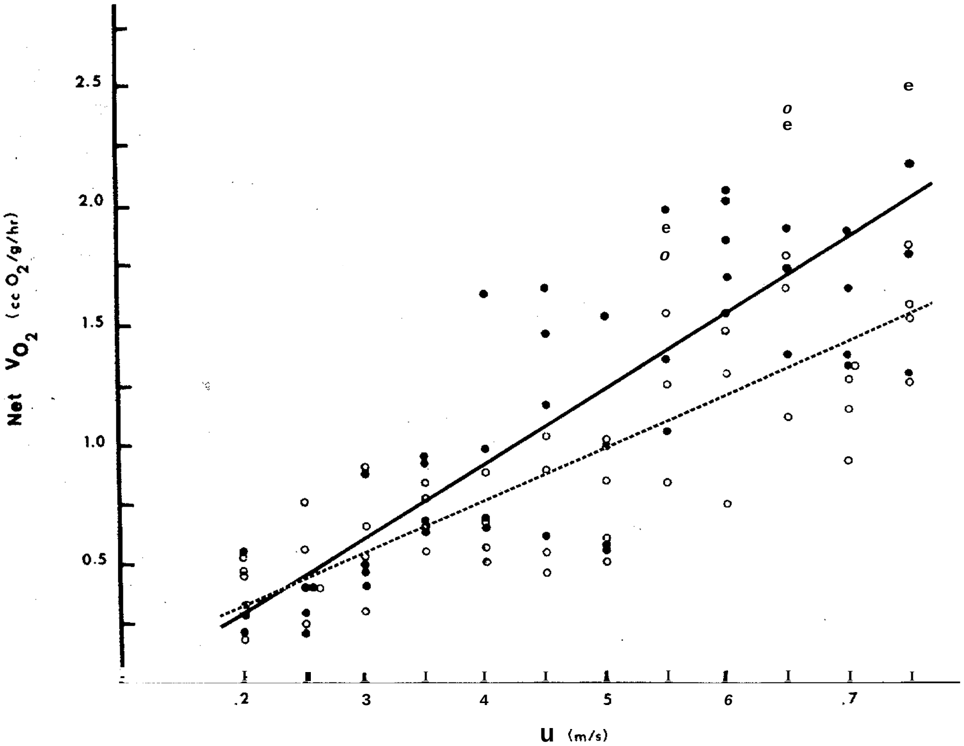

Fig. 1. Mass-specific oxygen consumption, net $\dot{V}_{O_2}$, as a function of swimming velocity, U, for muskrats in water temperatures of 25 (●——●) and 30 (○– – –○)°C.

(Robinson *et al.*, 1976; Chappell, 1980a), while measurements on the pelage of mammals shows a direct relationship between the convection coefficient and wind velocity (Chappell, 1980b).

The metabolic performance of a mammalian swimmer, such as the muskrat, appears to be influenced by a complex interaction of factors including swimming speed and water temperature. Since water places a more severe thermal stress on a homeotherm than air at the same temperature, the balance between heat production and loss for thermoregulatory maintenance in conjunction with exercise metabolism is not comparable to equal metabolic effort in air. Further studies of swimming effort and water temperature should elucidate a more comprehensive understanding of thermoregulation and exercise.

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