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THERMOREGULATION IN THE
MUSKRAT (ONDATRA ZIBETHICUS):
THE USE OF REGIONAL
HETEROTHERMIA

By

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ABSTRACT

THERMOREGULATION IN THE MUSKRAT (ONDATRA ZIBETHICUS):
THE USE OF REGIONAL HETEROTHERMIA

By

Frank E. Fish

Regional heterothermia, metabolic rates, and whole-body insulation were studied in six muskrats (Ondatra zibethicus), restrained in air and in water at temperatures of 20, 25, and 30°C. Appendicular temperatures were found to approach ambient temperatures for all temperatures in water and at 20 and 25°C in air. In air at 30°C, appendicular temperatures increased above ambient temperature after an average colonic temperature of 39°C was attained. Metabolic rates were higher in water than in air, while values of whole-body insulation were higher in air than water. High peripheral temperatures, due to vasodilation, decrease whole-body insulation and allow for increased heat dissipation, while peripheral temperatures approaching ambient temperature, due to vasoconstriction or counter-current heat exchanges, increase whole-body insulation maximizing heat conservation. The causative factor, for the differential responses of muskrats in air and water, was considered to be the higher thermal conductivity of water than air.

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TABLE OF CONTENTS

	Page
LIST OF TABLES	iv
LIST OF FIGURES	v
INTRODUCTION	1
METHODS	3
Experimental Animals	3
Experimental Procedure	3
Temperature	4
Weight-Specific Metabolic Rate	5
Whole-Body Insulation	7
Statistical Procedures	8
RESULTS	9
Regional Body Temperatures	
Weight-Specific Metabolic Rate	14
Whole-Body Insulation	19
Correlation Analyses	22
DISCUSSION	24
APPENDIX A. REGIONAL BODY TEMPERATURE	36
LITERATURE CITED	37

LIST OF TABLES

Table	Page
1. Results of correlation analyses between whole-body insulation and regional body temperatures for each body region of muskrats exposed to environments of air and water	23
2. Mean regional body temperatures (\pm one standard error) for all muskrats exposed to environmental media of air and water at T_a 's of 20, 25, and 30°C	36

LIST OF FIGURES

Figure	Page
1. Mean regional body temperatures, T_b , plotted against ambient temperature, T_a , for all muskrats in air and in water	11
2. Regional body temperatures of a restrained muskrat during exposure to a T_a of 30°C, starting 2 hours after the beginning of the experiment	16
3. Resting metabolic rate for all muskrats as a function of the ambient temperature, T_a , in air and in water . . .	18
4. Whole-body insulation for all muskrats plotted as a function of the ambient temperature, T_a , in air and in water	21

INTRODUCTION

The sparsely haired appendages of various mammals may act as potentially major sites of heat loss (conduction, convection, radiation) due to their relatively high surface-to-volume ratio and sparse pelage insulation. These sites of heat loss may thus be of serious consequence to mammals that maintain a semi-aquatic existence. Since water has a high heat capacity and is at least 25 times more conductive than air at the same temperature (Weast, 1971), these homeotherms are confronted with heavy thermal demands.

Physiologically, semi-aquatic mammals may cope with the high thermal conductivity of water by allowing the temperature of sparsely haired appendages to fall close to ambient temperature. Because heat is lost in direct relation to the thermal difference between the surface of the skin and the environment (Bartholomew, 1972), there is a reduction in the rate of heat dissipation from the appendages by permitting the appendage to approach ambient temperature. Conversely, excess heat may be lost through the skin of the appendage by increasing peripheral blood flow from the body core. Hammel (1968) has stated, that in endotherms with core temperature greater than ambient, the "control of blood flow to the periphery can readily regulate the flow

of heat from core to skin, and is the only controllable way to distribute internal heat to the skin." The phenomenon in which different temperatures are maintained in different parts of the body is termed regional heterothermia (Hill, 1976). This response has been found to be common in both aquatic and terrestrial mammals.

The purpose of this study was to examine the role of regional heterothermia in the thermoregulation of a semi-aquatic mammal with regard to changes in whole-body insulation, and differential responses to environments of air and water. For this study, the muskrat (Ondatra zibethicus) was selected as the experimental animal, due to its semi-aquatic nature (Johnson, 1925; Errington, 1962) and sparsely haired appendages which comprise less than 10% of the total surface area (Johansen, 1962a). It was hypothesized that there is (i) a difference in regional body temperatures (e.g., tail, feet) of muskrats in water and in air over the same temperature range, (ii) an increase in the metabolic rate for muskrats in water over those in air, and a decrease in the whole-body insulation for animals in water compared to those in air, and (iii) an inverse correlation between the temperature of the appendages and whole-body insulation.

METHODS

A. Experimental Animals

Four male and two female muskrats (Ondatra zibethicus) were live-trapped in Ingham and Clinton Counties, Michigan, during the spring and summer of 1976. They ranged in weight from 485 to 1152 g (mean: 869 g) during the period of testing. The animals were initially maintained outdoors in an open-air enclosure for a period of one week after capture to acclimate them to captivity. The enclosure was equipped with an artificial pond, with running water, and a nest box with wood-shaving bedding. A diet of cattail (Typha sp.) roots and Wayne Lab-Blox was provided. Following the initial one-week period, the muskrats were housed indoors in separate metal cages (51x36x31 cm), with wood-shaving bedding. Water and food were supplied ad libitum, with the food being Wayne Lab-Blox supplemented with dog food (Perk Food Co.), carrots, and apples. Average air temperature in the colony was 21°C, and the light cycle was natural.

B. Experimental Procedure

Regional body temperatures (T_b), resting metabolic rate (\dot{V}_{O_2}), and whole-body insulation of each muskrat were examined in environmental

media of air and water at ambient temperatures (T_a) of 20, 25, and 30°C. Muskrats were tested individually in a metabolic chamber, while under restraint. During tests in air, sealed cartons were placed within the chamber to reduce the chamber air volume and corresponding equilibrium time, as calculated by the formula of Lasiewski et al. (1966). In no way did the cartons interfere with movements by the muskrat. For tests made in water, the chamber was filled with water to 74% of its volume.

Each muskrat was fasted for at least 24 hr prior to testing to establish a post-absorptive state. The muskrat was anesthetized with Metophane (Pitman-Moore Inc.), and secured to a Plexiglas restraining board. Three leather straps fastened to the board were positioned to restrain the cervical, thoracic, and pelvic regions of the muskrat. The board was shaped to allow the legs to hang freely, while small holes in the board allowed for the free movement of water or air between the under-surface of the muskrat and the board.

C. Temperature

Regional body temperatures of the dorsal skin (center of dorsal abdomen; T_{ds}), foreleg (posterior surface of lower wrist; T_{fl}), hindfoot (plantar surface; T_{hf}), proximal tail (4 cm from the base in dorsal keel; T_{pt}), and distal tail (4 cm from tip in dorsal keel; T_{dt}) were measured using thermocouples constructed from 36-gauge, Teflon-insulated copper and constantan wires (Omega Engineering Inc.). Thermocouples were implanted subcutaneously by first forcing a 20-gauge hypodermic needle through a fold in the integument, then threading the wires through the needle and removing the needle. Colonic temperature (12 cm

into the colon; T_c) was measured using a thermocouple constructed from 30-gauge copper and constantan wires soldered at the tip and threaded through polyethylene tubing (2.08 mm OD). All body temperatures were monitored continuously with a 12-point Honeywell Electronik 15 potentiometer. T_a 's were monitored with a thermistor probe connected to a Yellow Springs Instruments Tele-Thermometer Model-43, located in a corner of the metabolic chamber 10 cm above the floor.

D. Weight-Specific Metabolic Rate

The metabolic chamber was constructed from a 70.4 liter glass aquarium and was fitted with a removable Plexiglas lid. The inner dimensions of the chamber were 75.3x31.5x29.7 cm. The lid was fitted with inflow and outflow tubes for air flow and ports for the passage of thermocouple wires and thermistor probe. A flexible rubber gasket was attached to the rim of the chamber and petroleum jelly applied to form an air-tight seal with the lid. The lid was clamped in place using braces. Brackets, inside the chamber, supported the restraining board and muskrat, with the animal's head angled 11° upward from the horizontal. This arrangement allowed the experimental animal to breathe while, during some tests, the majority of the body was submerged in water. During all tests in water, a Beckett N-100 submersible pump was employed to circulate water in the chamber at a rate of 122 l/hr. The metabolic chamber was kept inside a Sherer Model CEL 25-7 Controlled Environmental Chamber to control the T_a .

Weight-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, CO₂-free air flowing out of the metabolic chamber was monitored continuously with a Beckman G-2 paramagnetic oxygen analyzer and recorded on a Honeywell Elektronik 15 potentiometer. Ascarite (A.H. Thomas Co.) and Drierite (W.A. Hammond Co.) were used to absorb CO₂ and water vapor, respectively, from the air flow. The rate of air flow entering the metabolic chamber was measured with a calibrated Gilmont Model 1300 flowmeter. The average flow rate ranged in different tests from 1803 to 3061 cc/min for dry air at STP. Before entering the metabolic chamber, the air flow was passed through a copper coil immersed in a water bath inside the environmental chamber. This allowed the air flow to equilibrate to the desired T_a. Oxygen consumption was calculated by the procedure of Depocas and Hart (1957) and Hill (1972) and expressed as cc O₂(STP)/g/hr.

The experimental animal remained in the metabolic chamber after placement of the thermocouples for a period of at least 1 hr prior to testing to allow for the effects of the anesthetic to diminish and for adjustment to T_a, which had been established previously. \dot{V}_{O_2} and T_c were monitored until the muskrat had reached a steady state condition. The steady state condition was considered to be attained when there was no net change in T_c and \dot{V}_{O_2} . Before data were recorded after steady state had been reached, the air in the metabolic chamber was allowed time to mix with incoming air at an equilibrium level of 90%, as calculated by the formula of Lasiewski et al. (1966). The chamber equilibrium time for each environmental medium tested was 40 min in air

or 20 min in water. The average total time that the muskrat spent in the metabolic chamber was 4 hr with the time until equilibrium had been attained ranging from 1 to 2 hr.

The Winkler method of measuring dissolved oxygen (Welch, 1948) was employed to determine if diffusion of oxygen between the air flow and water contributed a possible error in the measured oxygen consumption. Water samples were drawn prior to and immediately after testing, and the difference in oxygen concentration between the two samples calculated. The net oxygen exchange between air and water was found to be less than 0.5% of the \dot{V}_{O_2} of the muskrat, and was considered to represent no significant error and was not corrected for.

E. Whole-Body Insulation

The whole-body insulation was calculated following the method of Scholander et al. (1950), in which insulation = $(T_c - T_a) / \dot{V}_{O_2}$. The insulation was corrected, by the method of Dawson and Schmidt-Nielsen (1966) for net changes in T_c during the test period, indicating a change in the heat content of the body. The change in the total heat content of the body was calculated after adjustment of the body weight by subtracting the weight of the appendages, which had temperatures approaching T_a . The net change in the heat content of the body was computed by the product of the adjusted weight of the body, the net change in T_c , and the specific heat of the body of $0.83 \text{ cal g}^{-1} \text{ } ^\circ\text{C}^{-1}$. The change in heat content was subtracted from \dot{V}_{O_2} , when the net change in T_c was positive, and was added to \dot{V}_{O_2} , when the net change in T_c was negative.

F. Statistical Procedures

Statistical comparisons were made for data on body temperatures with a split-plot, randomized block design on a 2(environmental media)x 3(T_a) factorial; one-way analysis of variance (AOV), and for \dot{V}_{O_2} and whole-body insulation with a randomized block design on a 2x3 factorial, one-way AOV. Individual contrasts were made using Student-Newman-Keuls' test (SNK). Correlations between whole-body insulation and the regional body temperatures were calculated using correlation analysis. Differences were considered significant at $P \leq .05$.

RESULTS

A. Regional Body Temperatures

The mean temperatures for each of the six body regions (T_b) in relation to ambient temperature (T_a) in air and in water are summarized in Figure 1 and listed in Appendix A. Using a one-way AOV, it was found that the interaction of T_a and environmental medium as factors affecting T_b was statistically significant ($P < .001$), inferring that T_b 's were dependent on both T_a 's and environmental media. Due to the magnitude of the interaction, the effects of T_a and environmental media on T_b were examined independently. The T_b 's of all the body regions were found to increase in direct response to increases in T_a , regardless of the environmental medium. However, the temperature responses for each of the body regions showed significant differences between the environments of air and water ($P < .001$).

T_c and T_{ds} responded similarly to all treatment combinations. A maximum difference of 1.1°C between the mean body temperatures of T_c and T_{ds} occurred in air at 20°C T_a . Only slight rises in temperature were recorded for the colon and dorsal skin from 20 to 30°C T_a in air and from 25 to 30°C in water. Exposure to 20°C in water

Figure 1. Mean regional body temperatures, T_b , plotted against ambient temperature, T_a , for all muskrats in air and in water. The dashed lines are lines of equality between T_b and T_a .

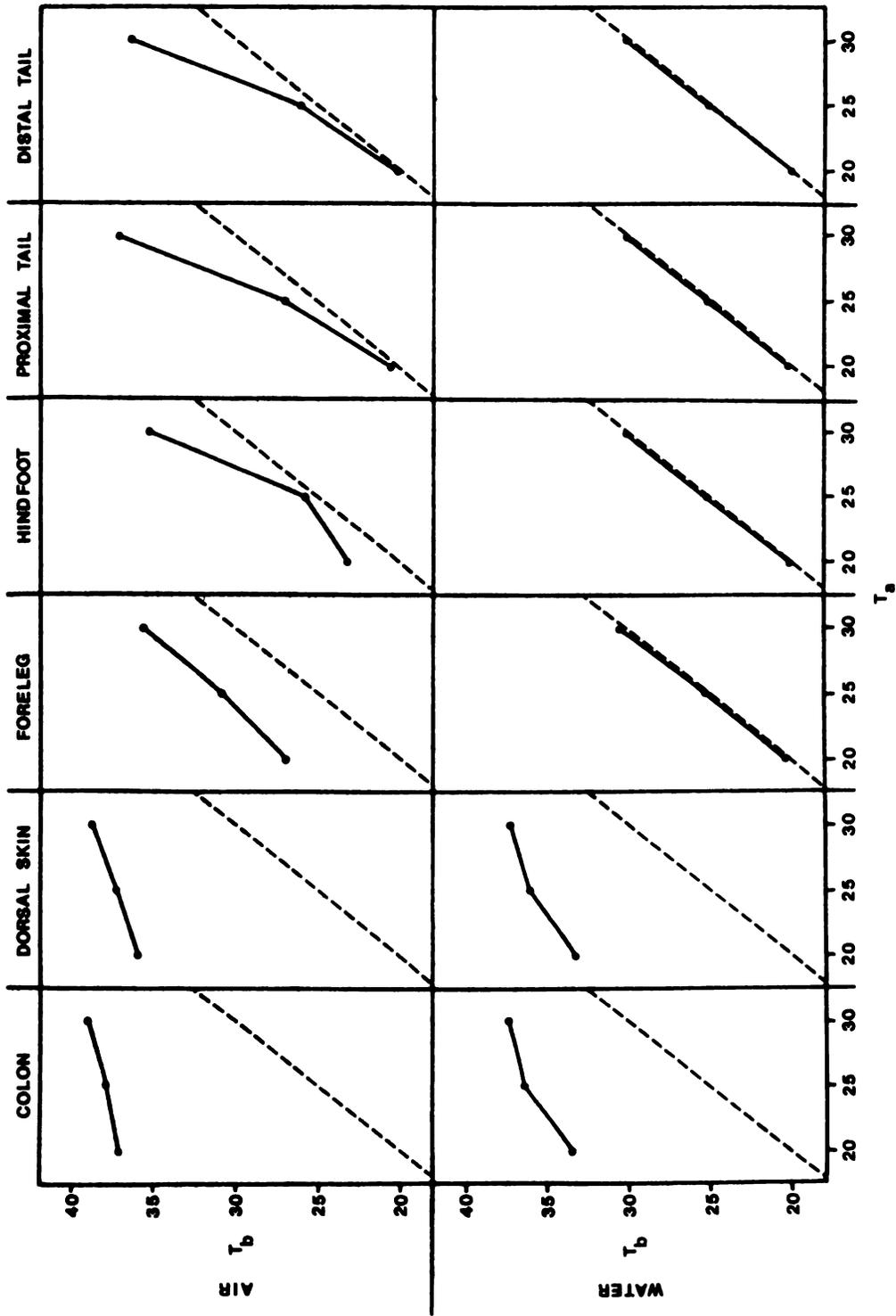


Figure 1

depressed mean T_c and T_{ds} to values of 33.6 and 33.4°C, respectively, which represented a sharp decline from values of 36.4 and 36.1°C at a T_a of 25°C. In one case, one individual muskrat maintained a steady state T_c of 28.5°C in water at 20°C T_a . Such results are similar to those observed by Hart (1962), in which the T_c for unrestrained muskrats tested in water fell at T_a 's of 20°C and below. The depressed T_c for muskrats in water at 20°C was presumed to indicate that the animals had attained a hypothermic state.

Appendicular temperatures, as represented by foreleg, hindfoot, proximal tail, and distal tail in Figure 1, varied substantially over the range of T_a 's for both air and water. These T_b 's were found by SNK to increase significantly as T_a increased ($P < .05$) and were significantly different by SNK from T_c and T_{ds} under all conditions ($P < .05$). Substantial increases of appendicular temperatures above T_a at certain T_a 's were assumed to indicate increased peripheral blood flow due to vasodilation at such T_a 's. Johansen (1962a) demonstrated experimentally that tail temperatures of approximately 35°C were due to increased peripheral blood flow caused by vasodilation.

In air, T_{f1} remained significantly higher than the other appendicular temperatures at T_a 's of 20 and 25°C with means of 27.1 ± 1.5 and 30.9 ± 1.2 °C, respectively ($P < .01$). Sample calculations, based on rough estimates of foreleg surface area and temperature distribution using the formulas of Calder and King (1974) for conductive and convective heat transfer and a thermal conductivity coefficient of tissue of $0.0011 \text{ cal s}^{-1} \text{ cm}^{-1} \text{ }^\circ\text{C}^{-1}$ (Schmidt-Nielsen, 1975), indicated that heat conduction from the body to the foreleg would not be sufficient to maintain a high T_{f1} against heat loss due to free or forced convection.

Heat transfer by conduction through the appendage was calculated to occur at a rate of 0.065 cal/min in air at 20°C T_a , while under these conditions the rates of heat loss from the surface of the skin by free convection and forced convection at a wind velocity of 20 cm/sec were 0.258 and 0.973 cal/min, respectively. A probable explanation is that, at all T_a 's in air, blood flow persists to the foreleg supporting an elevated T_{f1} by conductive and circulatory convective heat transfer. The mean T_{hf} at 20°C in air was 23.3±2.5°C. The elevation of this temperature above T_a was produced by the response of a single muskrat, which maintained an average T_{hf} of 35.5°C. Exclusion of this individual would yield a mean T_{hf} of 20.9±0.4°C, which would be only slightly higher than T_{pt} and T_{dt} for the same conditions. The two tail temperatures remained close to T_a for tests in air at 20°C. Although only small increases above T_a were observed for mean T_{hf} , T_{pt} , and T_{dt} in air at 25°C, one individual demonstrated peripheral warming with an elevated T_{pt} of 32.7 and T_{dt} of 31.9°C.

In air at 20 and 25°C, no large fluctuations were observed in T_b 's before or during the attainment of steady state by muskrats tested in the metabolic chamber. However, prior to the experimental animals' reaching steady state in air at 30°C T_a , T_c increased gradually, while T_{hf} , T_{pt} , and T_{dt} remained slightly above T_a . At some point after T_c had risen to a mean of 39.0°C, all appendicular temperatures were observed to increase rapidly, while T_c remained relatively constant or showed a slight decrease. The appendicular temperatures exhibited small fluctuations after T_c had ceased to increase. The temperature record for a typical muskrat in air at 30°C illustrating the relationship of the central body temperatures with the increased temperature of the

appendages is shown in Figure 2. T_{fl} , T_{hf} , T_{pt} , and T_{dt} for all muskrats ranged from 5.4 to 7.2°C above T_a , and these elevated temperatures are believed to be the result of increased peripheral blood flow due to vasodilation. Of particular interest is that peripheral vasodilation in muskrats was only elicited when animals had a T_c of at least 39°C. This is consistent with the data reported by Johansen (1961) in which tail temperature increased to 35 to 37°C after muskrats had been subjected to a positive heat load or exercise, and circulation of the tail kept rectal temperature below 39°C.

In contrast to tests in air, all appendicular temperatures for muskrats tested in water were very similar and closely approximated all T_a 's, with a maximum difference of 0.7°C for T_{fl} at 30°C.

B. Weight-Specific Metabolic Rate

The results on \dot{V}_{O_2} for muskrats in air and in water are summarized in Figure 3. AOV showed a significant interaction between the environmental media and T_a 's ($P < .01$). Therefore, \dot{V}_{O_2} varied in response to T_a and the environmental medium. Restrained muskrats in water had a significantly higher \dot{V}_{O_2} than animals in air over the same range of T_a ($P < .001$). In water, \dot{V}_{O_2} ranged from 91% higher than \dot{V}_{O_2} in air at 25°C to 34% higher at 30°C. The \dot{V}_{O_2} observed for a T_a of 30°C in water was revealed by SNK to be significantly lower than the other values in water ($P < .01$), and represented a reduction of 0.34 cc O_2 /g/hr from the value reported for 25°C T_a . In contrast, the values for \dot{V}_{O_2} in air remained relatively stable for all T_a 's, with no significant differences between values.

Figure 2. Regional body temperatures of a restrained muskrat during exposure to a T_a of 30°C, starting 2 hours after the beginning of the experiment. Temperature changes of the colon (● ●), dorsal skin (○----○), foreleg (■—■), hindfoot (□----□), proximal tail (▲—▲), and distal tail (△----△) are recorded in 10-min intervals. Note the sharp rise in appendicular temperatures, indicating peripheral vasodilation, with a simultaneous decrease in the temperature of the colon and dorsal skin.

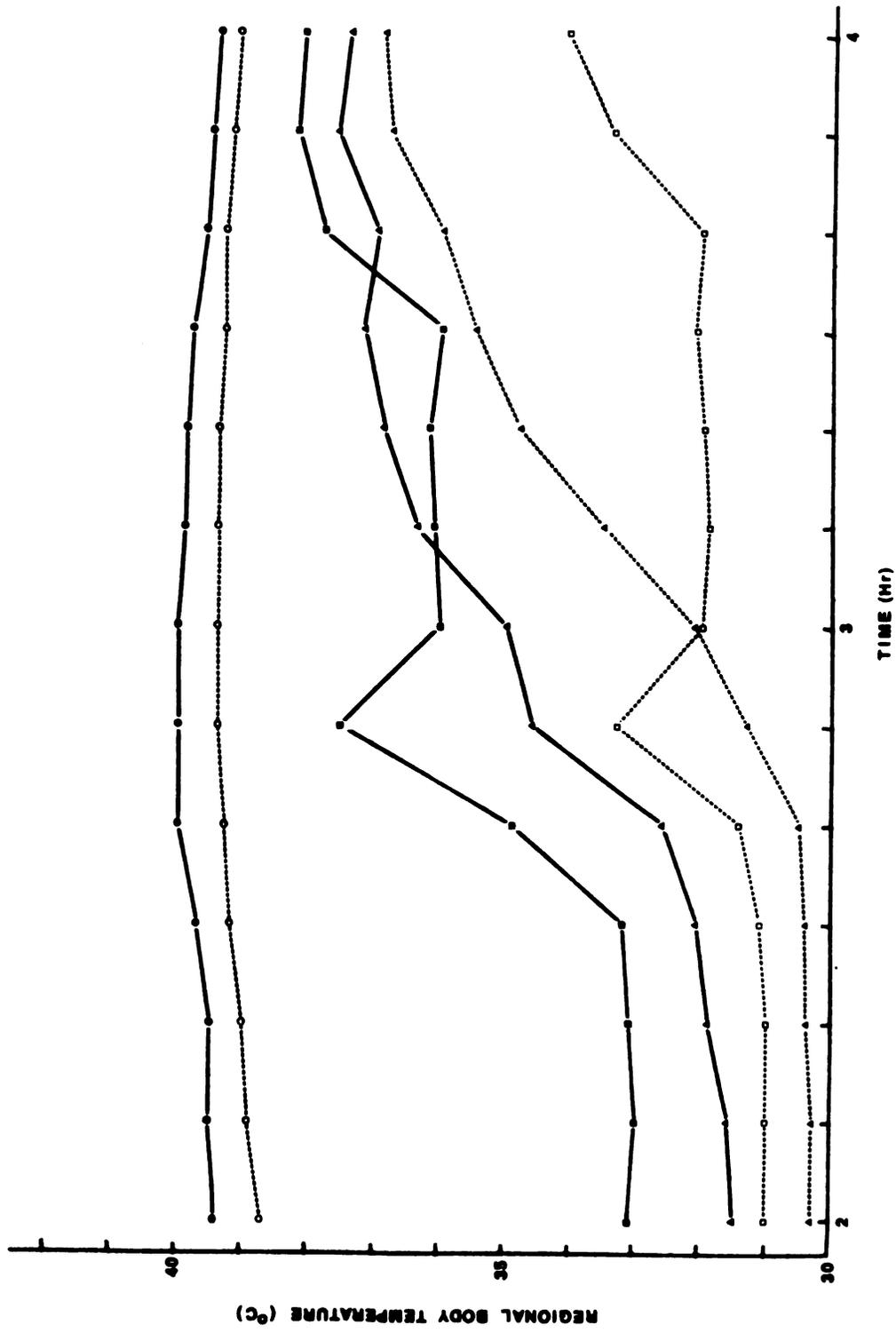


Figure 2

Figure 3. Resting metabolic rate for all muskrats as a function of the ambient temperature, T_a , in air (●—●) and in water (○----○). Symbols represent means for each treatment combination; vertical lines represent \pm one standard error (SE).

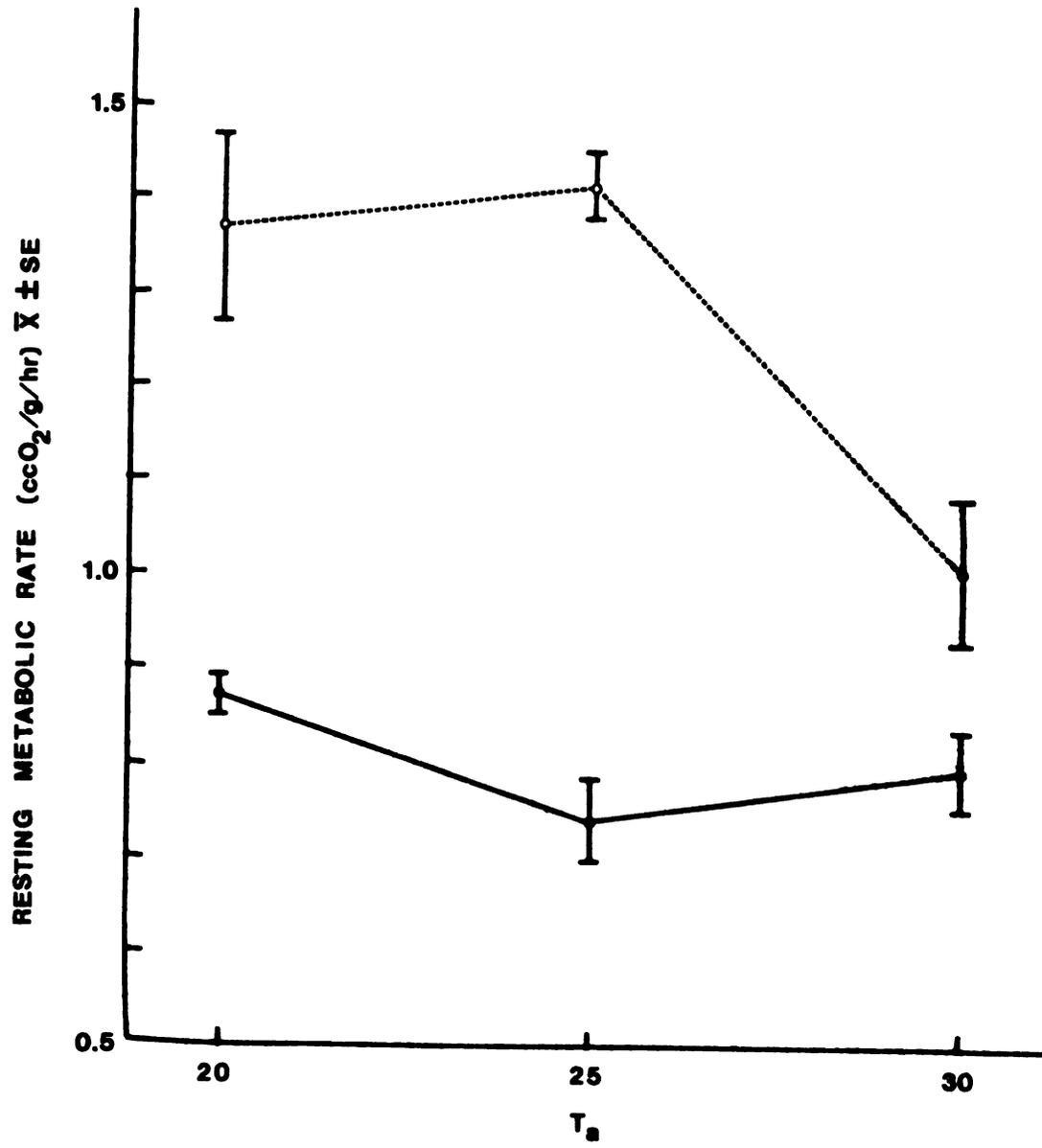


Figure 3

C. Whole-Body Insulation

Whole-body insulation plotted against T_a in air and in water is illustrated in Figure 4. The insulation was dependent on both the T_a and environmental medium examined as indicated by AOV ($P < .001$). The range of insulative values for muskrats restrained in water was significantly lower than those values calculated for air for all T_a 's tested ($P < .001$). This appears to be the direct result of the different thermal conductivities and convectivities of the two media. At 20 and 25°C T_a , the difference in whole-body insulation between air and water was essentially constant at 11.21 °C/cc O_2 /g/hr. This value represents a difference of 128% for the insulation of muskrats in air over the insulation for the same animals in water. At 30°C T_a in air, the mean whole-body insulation was 11.25 ± 0.3 °C/cc O_2 /g/hr, which represents a reduction of 42% from the insulation of 25°C in air. It is noteworthy that under these particular conditions, there was a corresponding increase in the temperature of the appendages. Although the \dot{V}_{O_2} in air did not significantly change between 25 and 30°C T_a , the colonic-ambient temperature differential, $T_c - T_a$, decreased, thus resulting in a smaller calculated whole-body insulation. No similar reduction for insulation was recorded for animals in water at a T_a of 30°C and, correspondingly, increased vasodilation of the appendages was not indicated. Whole-body insulation decreased at a constant rate in water as T_a increased, with a reduction of 2.3 °C/cc O_2 /g/hr for the range of T_a 's tested.

Figure 4. Whole-body insulation for all muskrats plotted as a function of the ambient temperature, T_a , in air (●—●) and in water (○----○). Symbols represent means for each treatment combination; vertical lines represent \pm one standard error (SE).

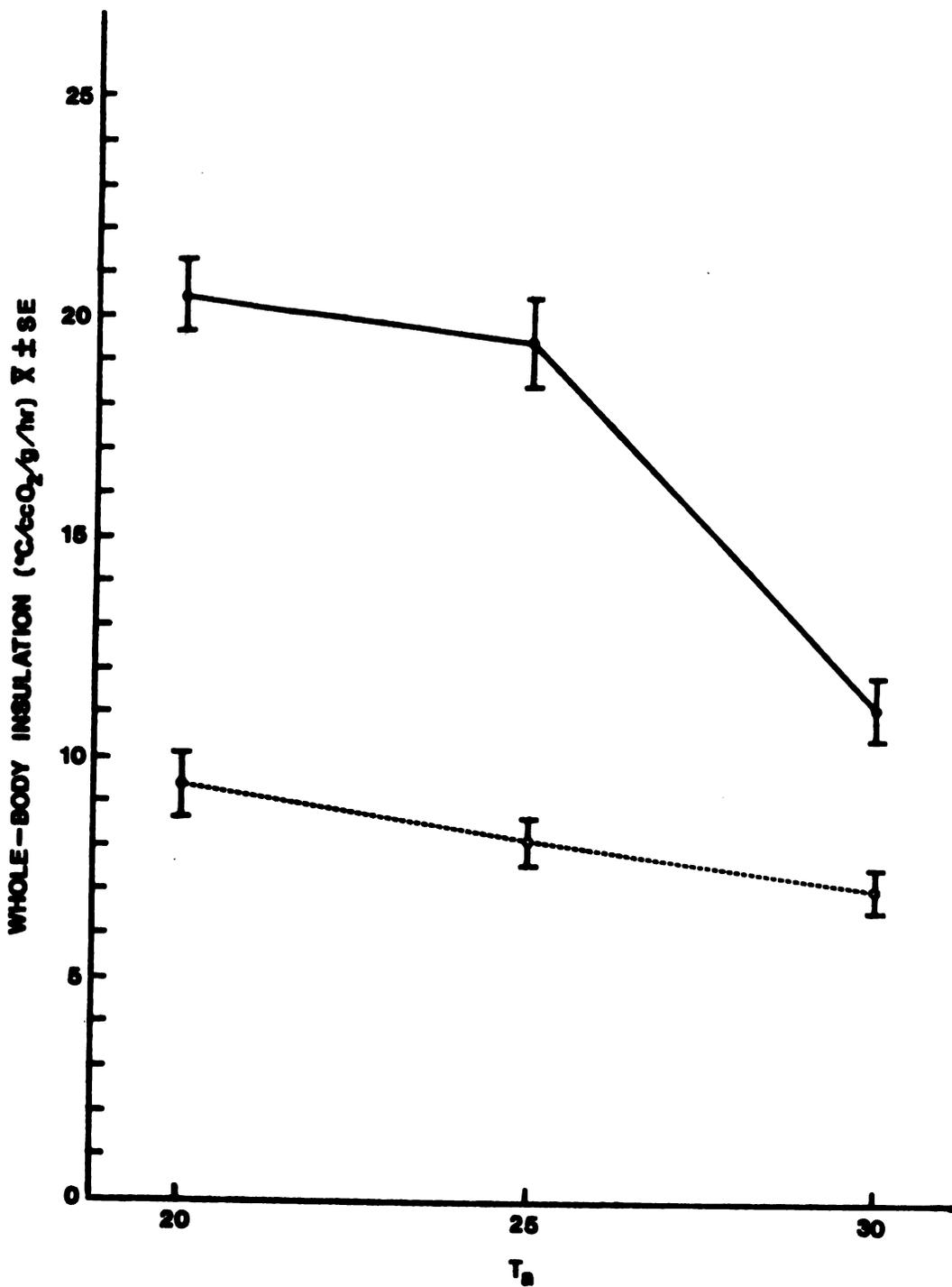


Figure 4

D. Correlation Analyses

The results of correlation analyses between whole-body insulation and regional body temperatures for muskrats exposed to environments of air and water are presented in Table 1. With the exception of T_c and T_{ds} in water, all T_b 's in air and water were significantly correlated with whole-body insulation ($P < .05$). In water, all appendicular temperatures had higher coefficients of correlation as compared to the two central body temperatures, while in air, only T_{hf} , T_{pt} , and T_{dt} were higher. The negative coefficients of correlation for all T_b 's except T_c in water, indicate that there is a decrease in the whole-body insulation with increasing T_b . From these results, it is apparent that changes in the temperature of the appendages are inversely associated with changes of the whole-body insulation of muskrats, and are at least partially responsible for the lability of the insulation. For muskrats in air, increases in appendicular temperatures, indicating increased peripheral blood flow, apparently allow for increased heat dissipation through the appendages, decreasing the over-all insulation of the body. Since no vasodilation is apparent in water for the T_a 's studied, only a slight reduction in whole-body insulation occurs with increasing appendicular temperatures are correspondingly lower (but still significant), with the conservation of heat being maximized

Table 1. Results of correlation analyses between whole-body insulation and regional body temperatures for each body region of muskrats exposed to environments of air and water.

Body Region	Environmental Medium	Coefficient of Correlation r
Colon	Air	-0.547*
	Water	0.009
Dorsal Skin	Air	-0.686**
	Water	-0.013
Foreleg	Air	-0.638**
	Water	-0.584*
Hindfoot	Air	-0.722**
	Water	-0.592**
Proximal Tail	Air	-0.878**
	Water	-0.588*
Distal Tail	Air	-0.905**
	Water	-0.591**

* P < 0.05

**P < 0.01

DISCUSSION

Irving and Krog (1955) demonstrated that peripheral cooling was not a characteristic of the entire body surface, but rather a property of the extremities for well furred northern mammals. The lability of temperature for the appendages has been well documented for a variety of aquatic mammals, including the muskrat (Johansen, 1961, 1962a; Shcheglova, 1964).

In the present study, restrained muskrats tested in environmental media of air and water at T_a 's of 20, 25, and 30°C demonstrated that the temperatures of various body regions were highly variable and under a certain amount of vasomotor control. Of particular importance were the sparsely haired appendages, which proved to be the most labile in their temperatures. For animals tested in air, T_a increased from 20 to 30°C, and appendicular temperatures increased by 8.6 to 16.4°C. Correspondingly, mean T_c rose from 37.1 to 39.2°C, while the mean T_{ds} was held to within 1.1°C of T_c . In air at 20°C, the tail was found to have a temperature approximating T_a , but T_{fl} and T_{hf} remained 7.1 and 3.3°C higher, respectively. Vasodilation of the appendages as indicated by a significant increase in appendage temperature above T_a , was observed for all muskrats tested in air at

30°C T_a . However, vasodilation in the appendages was only apparent after the animals had attained an average T_c of 39°C, before which T_{hf} , T_{pt} , and T_{dt} approached T_a . After vasodilation in the appendages, T_c was observed to stabilize or decrease. In water, no vasodilation was observed over the range of T_a 's tested, and all appendicular temperatures remained close to T_a . Mean T_c and T_{ds} were found to be depressed in water at 20°C T_a , being 33.6 and 33.4°C, respectively, and remained below 39.0°C for the other T_a 's.

Johansen (1961) found rectal temperatures in muskrats to be between 37 and 39°C with no peripheral warming at T_a ranging from 0 to 20°C. At T_a 's above 25°C the tail temperature rose to 35 to 37°C, while blood flow increased by a factor of 100-180. In a later study, Johansen (1962a) found tail blood flow during vasodilation to increase by a factor of more than 400. The white rat in air has been shown to vasodilate the tail at T_a between 27 and 30°C, with blood flow rising from less than 5 ml to 40 ml of blood per 100 ml of tissue per min (Rand et al., 1965). This increase in blood flow to the tail was responsible for the dissipation of 25% of the total heat production. Johansen (1962a) stated that at T_a of approximately 20°C, the tail temperature of the muskrat fluctuated spontaneously and rapidly between 20 and 35°C. In the present study, tail temperatures were not observed to fluctuate, but remained close to a T_a of 20°C in both air and water. The increase in tail blood flow and corresponding temperature increase of muskrats in air stimulated to exercise or subjected to a positive heat load, observed by Johansen (1962a), were considered to be responsible for the prevention of heat accumulation in the body due to the high insulatory properties of the pelage. In

muskrats in air at 18-20°C, when the tail was immersed in ice water, tail skin temperature exhibited a rapid decline from over 30°C to 1°C. Johansen believed that such a response reduced heat dissipation as indicated by the stability of the rectal temperature. Shcheglova (1964) reported steady increases in the tail temperature of the muskrat from 5.7 to 24.4°C in water, and from 6.8 to 26.9°C in air as T_a 's increased from 0 to 35°C. MacArthur (1974) monitored body temperatures in free-living muskrats during the summer and observed that the deep body temperature increased during swimming and feeding activity. The body temperature in an adult male muskrat was reported to be as high as 39.9°C, and usually over 39.0°C during activity. This rise in deep body temperature was believed caused by the accumulation of excess metabolic heat due to activity of the skeletal muscles and the pelage insulation which facilitated heat storage. However, during swimming and diving for periods of 10 minutes or more in winter, muskrats showed a net decline in body temperature with only short-term increases during bursts of activity.

The thermoregulatory significance of heterothermic appendages of aquatic mammals has been studied by a number of investigators. These appendages, with their large surface area in proportion to the total body surface, represent a major avenue for the dissipation of excess heat from the well insulated body. In tests made on a single beaver (Castor fiber) it was concluded that the naked tail had a secondary function of controlling heat dissipation (Steen and Steen, 1965). As T_a increased from 16 to 25°C in air, the beaver was observed to increase rectal temperature from 37.0 to 39°C, and the

skin temperature at the tail tip increased from 16 to 35°C. Hyperthermia in air at 25°C was avoided when the tail was placed in water at 6°C. Heat loss from the tail to the water accounted for 20% of the total heat production. Morrison et al. (1974) estimated that heat loss through the paws of the sea otter (Enhydra lutra) could account for the dissipation of two-thirds of the heat load in water at 26°C and four-fifths in air at 22°C. Whittow et al. (1972) concluded that due to the high proportion of the total surface area represented by the flippers of the California sea lion (Zalophus californianus), they would be important in the control of heat loss. Irving et al. (1962) found that a considerable amount of heat was dissipated through the flippers of fur seals (Callorhinus ursinus) after being driven overland. Conversely, heat was conserved when flipper temperatures were found to be, at most, 4°C above the water temperature of 9°C for submerged seal pups. The dorsal fin of two species of dolphin has also been shown to function both for heat conservation and dissipation (McGinnis et al., 1972).

The weight-specific metabolic rates, \dot{V}_{O_2} , of muskrats in water were shown to be significantly higher than metabolic rates in air over the range of T_a , with differences ranging from 0.27 to 0.67 cc O_2 /g/hr at 30 and 25°C, respectively. \dot{V}_{O_2} for animals tested in air remained relatively stable for all T_a 's. Conversely, tests in water showed a marked decrease of 24% as T_a increased from 25 to 30°C.

The thermoneutral zone of fed muskrats in air has been reported to range from 10 to 25°C (McEwan et al., 1974), while in water the lower critical temperature was reported to be 30°C (Hart, 1962). Although only three T_a 's were tested in the present study, no detectable limits

to the thermoneutral zone were observed for tests in air, so that the restrained muskrats were believed to be in thermoneutrality at all test T_a 's. However, for an equitable comparison with the data of McEwan et al. (1974), a mean \dot{V}_{O_2} of 0.81 ± 0.03 cc O_2 /g/hr for T_a 's of 20 and 25°C was computed. This value was 17% lower than the \dot{V}_{O_2} of 0.97 cc O_2 /g/hr reported by Hart (1971) for muskrats in air. However, McEwan et al. (1974) reported mean resting metabolic rates in the thermoneutral zone as 83 kcal/kg/day for unfasted muskrats and 60 kcal/kg/day for 24-hr fasted animals. Recalculation of these values using a caloric conversion factor of 4.8 kcal/liter of oxygen at STP produces values of 0.72 cc O_2 /g/hr for unfasted and 0.52 cc O_2 /g/hr for 24-hr fasted muskrats, which are exceeded by the present \dot{V}_{O_2} by 11 and 35%, respectively. Since all muskrats in this study were fasted at least 24-hr prior to testing, the discrepancy may be due to the effect of the implanted thermocouples and restraint on the experimental animals. The \dot{V}_{O_2} in the present study was found to be comparable to Hart's (1962) data on muskrats in water at 30°C. Shcheglova (1964) found that the level of metabolism for muskrats in water was 18 to 30% higher than in air at T_a 's of 0 to 35°C. In the present study, the difference in the mean \dot{V}_{O_2} between air and water exceeded these values, with the \dot{V}_{O_2} in water being 34 to 91% higher than in air at T_a 's of 30 and 25°C. One muskrat was, however, found to have a \dot{V}_{O_2} in water exceeding that in air by only 4% at 30°C T_a . Such differences are probably due in part to the higher thermal conductivity of water compared to air. Both the platypus, Ornithorhynchus anatinus (Smyth, 1973), and sea otter, Enhydra lutra (Morrison et al., 1974) had a higher metabolic rate when exposed to water than air. Harbor seals

(Phoca vitulina), however, were found to have metabolic rates which were equal in both water and air (Irving and Hart, 1957; Hart and Irving, 1959). Such differences in the metabolic responses of semi-aquatic mammals may be due partly to differences in body size and to effects of non-wettable fur versus blubber for insulation.

The whole-body insulation of muskrats was found to be dependent on the T_a and environmental medium, and corresponded to changes in the temperature of the appendages. In water, the insulation was found to decrease slightly as T_a increased. T_{hf} , T_{pt} , and T_{dt} were found to be positively correlated with T_a and exhibited an inverse relationship to whole-body insulation in water. In air, a 42% reduction in whole-body insulation occurred between T_a 's of 25 and 30°C. This reduction corresponded to the significant increase in appendicular temperatures, indicative of peripheral vasodilation. All appendicular temperatures were highly and inversely correlated with whole-body insulation in air. Values of whole-body insulation were found to be 59 to 139% higher in air than in water. These differences are believed to be the result of the higher thermal conductivity of water than air. Immersion of the muskrat in water would also tend to reduce insulation by compression of the air layer trapped in the non-wettable fur. This would in effect decrease the length of the thermal gradient between the skin and the environment, causing a reduction in the effective insulation of the fur. Johansen (1962b) has shown that muskrats depleted of the insulative air layer lose heat at a faster rate than normal muskrats in water. Morrison et al. (1974) stated that sea otters in warm water showed a loss of buoyancy, indicating that water had penetrated the fur, facilitating heat transfer. Examination of muskrats

after the present tests in water showed that the air layer in the fur was maintained, except in regions in direct contact with the restraint apparatus.

As has been demonstrated for muskrats, various other semi-aquatic homeotherms have shown differences between the whole-body insulation measured in air and in water. Morrison et al. (1974) found that the minimum thermal conductance for sea otters in water at a critical temperature of about 7°C was 2.1 times greater than that in air at a critical temperature less than -19°C. In the present study, maximal insulation for muskrats in air was found to be 2.4 fold over that in water at 25°C. The total insulation of harbor seals during the summer was reported to be 2.1 times greater in air than in water at lower critical temperatures of 2 and 20°C, respectively (Hart and Irving, 1959). Both the Adelie penguin (Pygoscelis adeliae) and Gentoo penguin (P. papua) were shown to have insulations in air at 0°C approximately 1.5 times greater than those in water at 5°C (Kooyman et al., 1976). Morhardt et al. (1975) demonstrated that the rate of heat loss for small birds (Junco hyemalis, Passer domesticus) and rodents (Rattus norvegicus albino, Spermophilus beldingi, Heteromys desmaresteanus) immersed in water were 5 to 10 times as great as in air. The greater augmentation of heat loss from these animals, compared to semi-aquatic animals, would be expected due to the absence of specific adaptations of insulation to minimize the cooling effect of water. The water shrew (Sorex palustris), with a thermal conductance in water 4.5 times that in air, was found to differ in conductance from other shrews and small rodents only as a function of body size (Calder, 1969).

During testing, some of the muskrats were found to have tail temperatures which remained close to T_a for times of 5 hr or more. I am hesitant to believe that all blood flow is curtailed to the appendages for extended periods of time when their temperatures are equal to T_a . Although the heterothermic tissues of the appendage are still viable at low T_a 's (Miller, 1970), and operating at a lower metabolic rate, it might be advantageous to allow circulatory exchange with the body proper to occur. Circulation to the extremities could persist to allow for metabolic exchange while preventing undue heat loss by the use of a counter-current heat exchanger. This type of system for the muskrat would be similar in principle to the heat exchanger described by Scholander (1957). In such a system, arteries and veins run in close proximity to one another, thus allowing heat to be picked up from the arterial blood by the venous blood and short-circuiting the transfer of heat to the distal part of the appendage. This permits the retention of body heat without significant loss to the environment through the poorly insulated appendages. Further, heat may be dissipated across the appendages when appropriate by shunting warm blood from the arteries to superficial veins. This by-passes the heat exchanger and promotes heat transfer with the environment. Scholander and Schevell (1955) described such an arrangement in the flukes of porpoises. In this case, the counter-current exchanger consisted of a central artery with a surrounding ring of veins. The arrangement is such that when a large heat load must be dissipated, the blood pressure rise increases the diameter of the central artery, collapsing the venous ring, and reducing the effectiveness of counter-current heat exchange. The warm arterial blood is forced to return to the body through

superficial veins near the skin, which are normally constricted. Similar circulatory patterns have been described in the flippers of the northern fur seal and harbor seal, with thermoregulatory implications (Tarasoff and Fisher, 1970).

Irving and Krog (1955) were first to propose the existence of a counter-current heat exchanger in the tail of the muskrat. They based their conclusion on the occurrence of a sharp temperature gradient in the insulated base of the tail after the tail had been immersed in cold water. Thorington (1966) demonstrated that counter-current heat exchangers were common in the tails of a variety of rodents. Morphological characteristics in rodent tails, which were interpreted to function in thermoregulation, are the presence of shunts and anastomoses between arteries and veins, juxtaposition of arteries and veins, the presence of superficial and deep routes of venous return, and the distribution of valves in veins and arteriovenous anastomoses. The juxtaposition of arteries and veins would allow for the establishment of a heat transfer mechanism with heat exchange between the arterial and venous blood flows, retaining heat in the body. Arteriovenous anastomoses would function to shunt warm arterial blood to the superficial veins allowing for rapid heat dissipation. Although Thorington did not study the tail of the muskrat, because of the commonality of counter-current heat exchangers in a variety of diverse rodents, it would be logical to assume that such a morphological system exists in the muskrat. Latex injections which I performed on the arterial and venous systems of the muskrat tail have shown a similar configuration of the vascular network to the configurations in tails described by Thorington (1966). Of particular interest is the

presence of juxtaposition arteries and veins. Two central caudal veins were found to be dorso-lateral to the ventral caudal artery and in direct contact with the artery along the caudal vertebrae in the well insulated section of the tail. Numerous veno-venous shunts occurred between the two veins across the ventral side of the artery. The arterial system was elaborate with numerous branches and shunts along the length of the tail, while the venous system was shown to have superficial routes. The preceding anatomical evidence hints at the possibility of a counter-current heat exchanger present in the muskrat tail, although further morphological research is necessary.

The results of this study indicate that changes in the temperature of various body regions, especially the appendages, are inversely associated with changes in whole-body insulation. Appendicular temperatures approaching T_a tend to maximize the insulation of the body by reducing the rate of heat loss per unit of surface area. High appendicular temperatures, such as those observed in air at 30°C, indicated increased peripheral blood flow, and probably accounted for the sharp reduction in insulation, facilitating heat loss. This was most likely in response to the high central body temperatures representing a large heat load acquired by the muskrat. Such a situation may arise naturally due to high T_a , or increased metabolic heat production and storage during exercise, in which heat loss to the environment would occur through the appendages with a reduction in the over-all insulation. The higher thermal conductivity of water over air was surmised to be the causative factor in lower regional and central body temperatures, decreased whole-body insulation, and

increased weight-specific metabolic rates for muskrats in water as compared to the same animals in air.

Thus regional heterothermia, as occurs in the appendages of the muskrat, appears to serve as a heat regulator in which high peripheral temperatures, due to vasodilation, allow for increased heat dissipation, and low peripheral temperatures, because of vasoconstriction or counter-current heat exchangers, maximize heat conservation. This is important in that the sparsely haired appendages, as a result of their relatively large surface area, represent a major avenue for heat transfer from the body with its highly insulative pelage. Therefore, it would appear that regional heterothermia plays a necessary role in the thermal ecology of the muskrat, as a semi-aquatic homeotherm, by contributing to changes in whole-body insulation in response to a variable environment.

In summary, it has been demonstrated that there is a difference in the response of regional body temperatures of muskrats in air and in water, as well as an increase in the metabolic rate and decrease in the whole-body insulation in muskrats in water compared to those in air, and an inverse correlation between the temperature of the appendages and the whole-body insulation. Although it has often been inferred that changes in the temperature of the appendages may act to change the insulation of the body, this phenomenon has never been demonstrated for a semi-aquatic homeotherm in relation to its environment. It is presumed that the higher thermal conductance of water over that of air is responsible for the difference in the physiological adjustments made by the muskrat in that the pelage insulation alone is

insufficient to prevent general body cooling. Conversely, the pelage is capable of retarding heat loss from the body at high ambient temperatures in air and during exercise when heat storage would be deleterious to the muskrat. Thus the appendages of the muskrat appear to serve in thermoregulation allowing for both heat conservation and dissipation as required by the thermal state of the animal and the environment. The results of this study, while reinforcing the findings of previous studies, have increased our understanding of the role of regional heterothermia for a small semi-aquatic mammal, for which little is physiologically known.

APPENDIX A

REGIONAL BODY TEMPERATURE

Table 2. Mean regional body temperatures (\pm one standard error) for all muskrats exposed to environmental media of air and water at T_a 's of 20, 25, and 30°C.

Body Region	Environmental Medium	T_a		
		20°C	25°C	30°C
Colon	Air	37.1 \pm 0.5	38.0 \pm 0.5	39.1 \pm 0.2
	Water	33.6 \pm 1.2	36.4 \pm 0.5	37.4 \pm 0.4
Dorsal Skin	Air	36.0 \pm 0.5	37.4 \pm 0.4	38.8 \pm 0.3
	Water	33.4 \pm 1.1	36.1 \pm 0.4	37.3 \pm 0.5
Foreleg	Air	27.1 \pm 1.5	30.9 \pm 1.2	35.7 \pm 0.5
	Water	20.3 \pm 0.1	25.5 \pm 0.1	30.7 \pm 0.3
Hindfoot	Air	23.3 \pm 2.5	25.9 \pm 0.3	35.4 \pm 0.8
	Water	20.1 \pm 0.1	25.2 \pm 0.0	30.1 \pm 0.1
Proximal Tail	Air	20.8 \pm 0.3	27.1 \pm 1.2	37.2 \pm 0.3
	Water	20.2 \pm 0.1	25.3 \pm 0.0	30.1 \pm 0.1
Distal Tail	Air	20.2 \pm 0.1	26.4 \pm 1.1	36.5 \pm 0.3
	Water	20.2 \pm 0.1	25.2 \pm 0.0	30.1 \pm 0.1

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