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

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Abstract—1. 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.

2. Appendicular temperatures were found to approach ambient temperature at all temperatures in water and at 20 and 25°C in air.

3. In air at 30°C, appendicular temperatures increased above ambient temperature after an average colonic temperature of 39°C was attained.

4. High peripheral temperatures, due to vasodilation, decrease whole-body insulation and allow for increased heat dissipation, while peripheral temperatures approaching ambient temperature, resulting from vasoconstriction or counter-current heat exchange, increase whole-body insulation thus maximizing heat conservation.

5. The causative factor for the differential responses of muskrats in air and water was considered to be the higher thermal conductivity of water.

INTRODUCTION

The sparsely haired appendages of various mammals may act as major sites of heat loss through the processes of conduction, convection, and radiation, because of their relatively high surface-to-volume ratio and sparse pelage insulation. These potential sites of heat loss, which comprise a large percentage of the total surface of the body, may be of serious consequence to aquatic or semi-aquatic mammals. Since water is at least 25 times more conductive than air at the same temperature (Weast, 1971), such homeotherms may be confronted with heavy thermal demands.

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, such regional heterothermy (Irving & Krog, 1955) acts to reduce the rate of heat dissipation from the appendages.

The purpose of this study was to examine the role of regional heterothermy in changing whole-body insulation in a semi-aquatic mammal and to evaluate differential responses to environments of air and water. For this study, the muskrat ***(Ondatra zibethicus)*** was examined, due to its amphibious nature and sparsely insulated appendages which possess heterothermic characteristics (Johansen, 1962a). In comparison to other studies of **muskrat** thermoregulation, this investigation attempts to illustrate the interrelation between physiological parameters with variable environments.

MATERIALS AND METHODS

Experimental animals

Four male and 2 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 485–1152 g (mean: 869 g) during the period of testing. The animals were maintained outdoors in an open-air enclosure for a period of 1 week after capture to acclimate them to captivity. Following the initial 1-week period, the muskrats were housed indoors in separate metal cages (51 x 36 x 31 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.), apples, and carrots. Average air temperature in the colony was 21°C, and the light cycle was natural

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. 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 secuted to a Plexiglass 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 ambient medium.

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. 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 recording 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.

Weight-specific metabolic rate

The metabolic chamber was constructed from a 70.4 l glass aquarium and was fitted with a removable Plexiglas lid. The inner dimensions of the chamber were 75.3 × 31.5 × 29.7 cm. The lid was fitted with inflow and outflow tubes for air flow and ports for the passage of thermocouple wires and the 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, which 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 T_a.

Weight-specificoxygen 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 continuously with a Beckman G-2 paramagnetic oxygen analyzer and recorded on a Honeywell Electronik 15 potentiometer. Ascarite (A. H. Thomas Co.) and Drierite (W. A. Hammond Co.) were used to absorb CO_2 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 Hill (1972).

After placement of the thermocouples, the experimental animal remained in the metabolic chamber for at least 1 hr prior to testing to allow for the effects of the anesthetic to diminish and for adjustments to T_a. Data was recorded when no net change was observed for both T_c and $\dot{V}_{O_2}$ indicating steady state. The average total time that the muskrat spent in the metabolic chamber was 4 hr.

The Winkler method (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 for determination of dissolved oxygen. The net oxygen exchange between air and water calculated from these measures 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.

Whole-body insulation

Whole-body insulation was calculated following the formulation of Scholander *et al.* (1950): insulation = $(T_c - T_a)/\dot{V}_{O_2}$. The insulation was corrected for net changes in T_c during the test period by the method of Dawson & Schmidt-Nielsen (1966).

Statistical procedures

Statistical comparisons were made for data on body temperatures with a split-plot, randomized block design on a 2 (environmental media) × 3 (T_a) factorial, analysis of variance (AOV), and for $\dot{V}_{O_2}$ and whole-body insulation with a randomized block design on a 2 × 3 factorial, AOV

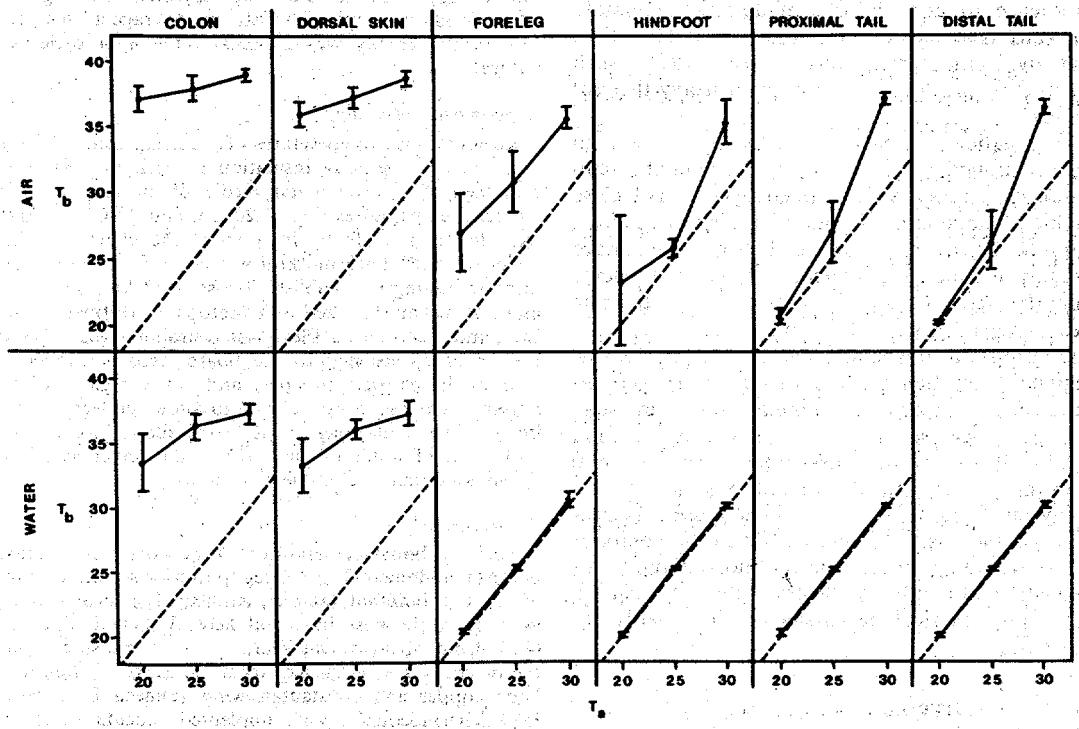

Fig. 1. Mean regional body temperature, T_b, plotted aginst ambient temperature, T_a, for all muskrats in air and in water. Vertical lines represent ± two standard errors. The dashed lines are lines of equality between T_b and T_a.

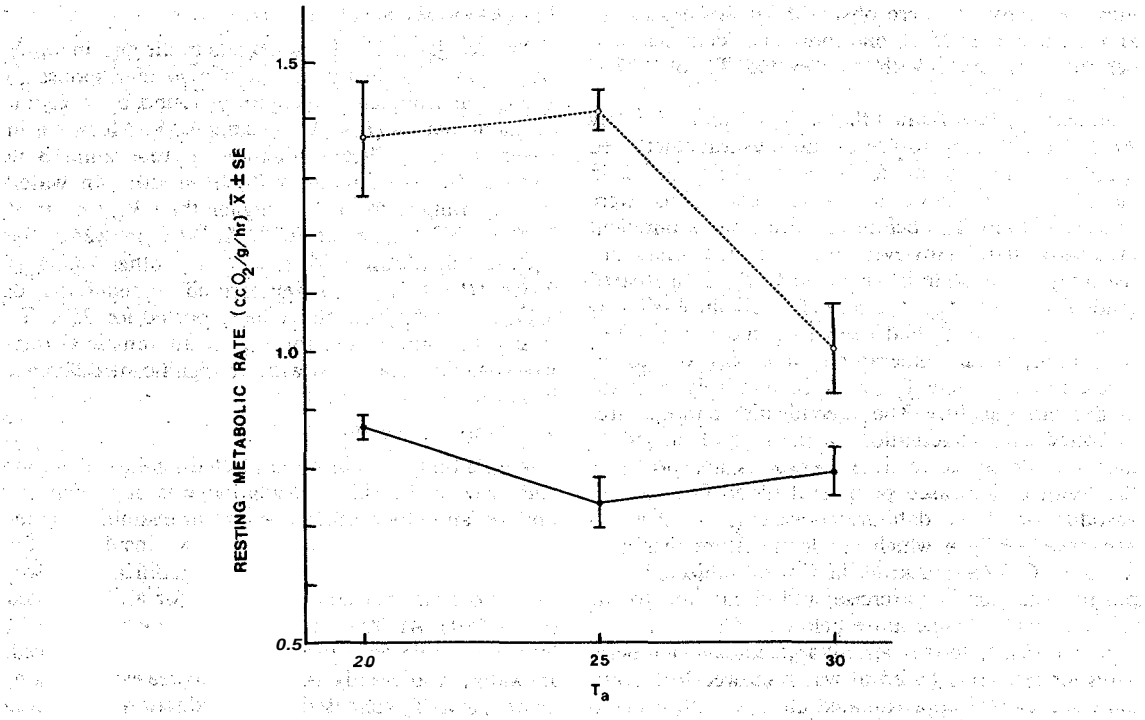

Fig. 2. Relationship between $\dot{V}_{O_2}$ and T_a, in air (●——●) and in water (○——○). Symbols represent means for each treatment combination; vertical lines represent ± one standard error (SE).

(Steele & Torrie, 1960). Individual contrasts were made using Student–Newman-Keds' test (SNK) (Steele & Torrie, 1960). Differences were considered significant at $P \leq 0.05$.

RESULTS

Regional body temperatures

The mean temperatures for each of the 6 body regions (T_b) in relation to ambient temperature (T_a) in air and in water are summarized in Fig. 1. Using AOV, it was found that the interaction of T_a and environmental medium as factors affecting T, was statistically significant ($P < 0.001$), 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,, 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 ($P < 0.001$).

T, and T,, were similar to each other under all treatment combinations. Only slight rises in temperature for colon and dorsal skin were recorded from 20 to 30°C T_a in air and from 25 to 30°C in water. Exposure to **20°C** in water depressed mean T, and T_{ds} to values of 33.6 and 33.4°C, respectively, which represented a sharp decline from values at 25°C T,. In one case, an individual muskrat maintained a steady state T_c of 28.5°C in water at 20°C T_a.

Appendicular temperatures, as represented by foreleg, hindfoot, proximal tail, and distal tail in Fig. 1, varied substantially over the range of T_a's for both air and water. These T_b's were found to increase significantly as T_a increased ($P < 0.05$) and were significantly different by SNK from T_c and T,, under all conditions ($P < 0.05$). Substantial increases of appendicular temperatures above T, at certain T_a's were assumed to indicate increased peripheral blood flow due to vasodilation at such T_a's.

In air, T_{fl} remained significantly higher than the other limb temperatures at T_a's of **20** and 25°C ($P < 0.01$). To determine if the high T_{fl} was due to blood flow or thermal conduction from the body, sample calculations were made to determine if the rate of conduction into the limb could be adequate to account for the rate of heat loss from the limb. Rates of heat loss was calculated using estimates of foreleg surface area and temperature distribution and using the formulas of Calder & King (1974) for conductive and convective heat transfer between limb and environment. Rate of conduction into the limb was calculated using a thermal conductivity coefficient of tissue of 0.0011 $cal\,sec^{-1}\,cm^{-1}\,°C^{-1}$ (Schmidt-Nielsen, 1975). The calculations indicated that heat conduction from the body to the limb would not be sufficient to maintain the high T,, against heat loss due to free or forced convection. Heat transfer by conduction through the limb 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 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_f, by circulatory convective heat transfer.

T_{hf}, T_{pt}, and T,, were not significantly different from T, for tests in air at 20°C. Although only small

increases above T, were observed for mean T_{ap}, T_{ap}, and T_{ap} in air at 25°C, one individual demonstrated peripheral warming with an elevated T_{ap} of 32.7°C and T_{dt} of 31.9°C.

Johansen (1962a) stated that at T, of approximately 20°C, the tail temperature of the muskrat fluctuated spontaneously and rapidly between 20 and 35°C. In air at 20 and 25°C, no large fluctuations were observed in any T_b's before or during the attainment of steady state. However, prior to the muskrat's reaching steady state in air at 30°C T_a, T_c increased gradually, while T_{bf}, T_{ap}, and T_{dt} remained slightly above T_b. When T_c had risen to a mean of 39.0°C, all apprendicular temperatures were observed to increase rapidly, while T_c remained relatively constant or decreased slightly. The appendicular temperatures exhibited small fluctuations after T_c had ceased to increase. These elevated temperatures are probably the result of increased peripheral blood flow due to vasodilation. These data are consistent with those of Johansen (1961) in which tail temperature increased to 35–37°C after muskrats had been subjected to a positive heat load or exercise, and circulation to the tail kept rectal temperature below 39°C.

In contrast to tests in air, all appendicular temperatures for muskrats tested in water showed little variance and closely approximated all T_a's, with a maximum difference of 0.7°C for T_{ap} at 30°C (Fig. 1).

Weight-specijic metabolic rate

The results of $\dot{V}_{O_2}$ for muskrats in air and in water are summarized in Fig. 2. $\dot{V}_{O_2}$ varied in response to T_a and environmental medium as found by a significant interaction ($P < 0.01$) using AOV. Muskrats in water had a significantly higher $\dot{V}_{O_2}$ than animals in air over the same range of T_a ($P < 0.01$). In water, the $\dot{V}_{O_2}$ ranged from 91% higher than $\dot{V}_{O_2}$ in air at 25°C to 34% higher at 30°C. At 30°C in water, the $\dot{V}_{O_2}$ was significantly lower than the other values in water ($P < 0.01$), 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 difference between values.

Whole-body insulation

Whole-body insulation is plotted against T_a in air and in water in Fig. 3. Insulation was dependent on both T_a and environmental medium examined, as indicated by AOV ($P < 0.001$). The insulation for muskrats restrained in water was significantly lower than those values calculated for air for all T_a's tested ($P < 0.001$). At 30°C T_a in air, a reduction of 42% from the whole-body insulation of 25°C was observed. In water, whole-body insulation decreased at a constant rate as T, increased, with a reduction of 2.3°C/cc O_2/g/hr over the range of T_a's tested

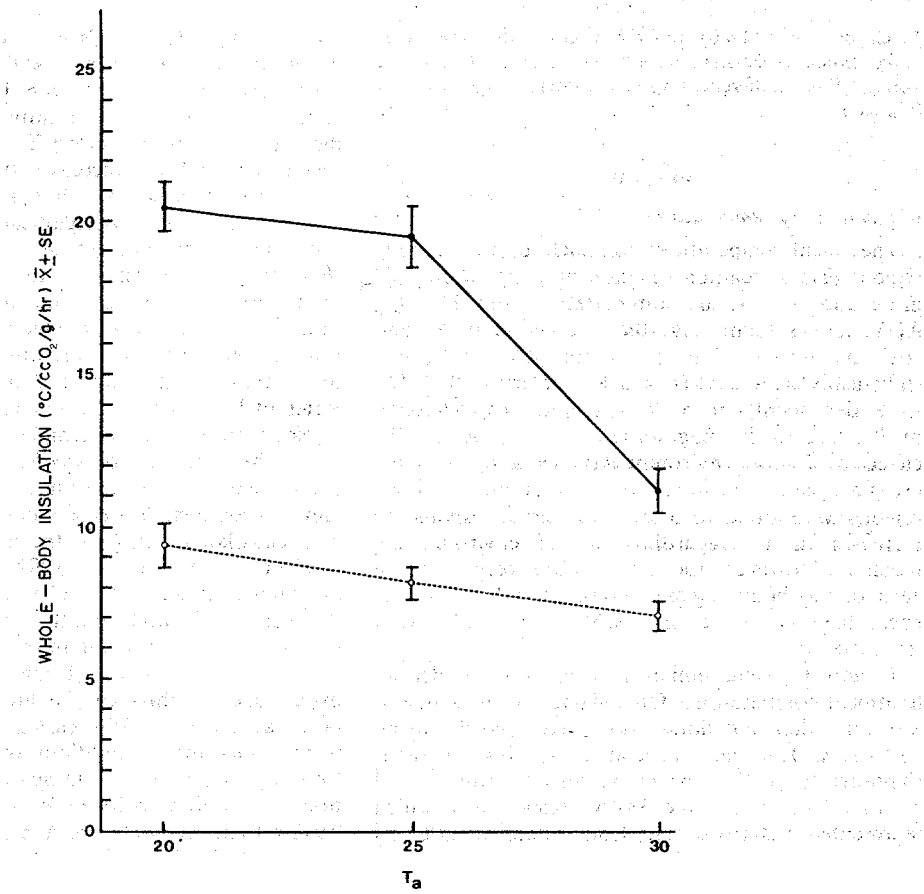

Fig. 3. Whole-body insulation plotted as a function of T_{ap} in air (●——●) and in water (○——○). Symbols represent means for each treatment combination; vertical lines represent ± one standard error (SE).

With the exception of T_c and T_{ds} in water, all T_b's in air and water were significantly negatively correlated with whole-body insulation ($P < 0.05$). In water, all appendicular temperatures had higher absolute coefficients of correlation than the two central body temperatures, while in air only T_{hf}, T_{pf}, and T_{dt} were higher. The negative coefficients of correlation for all T_b's except T_c in water indicate that whole-body insulation decreases with increasing T_b. For muskrats in air, increases in limb temperatures, indicated increased peripheral blood flow, apparently allow for increased heat dissipation through the appendages, decreasing the over-all insulation. 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, with the conservation of heat being maximized. These results indicate the relationship between T_b's and whole-body insulation.

DISCUSSION

Irving & Krog (1955) demonstrated that cooling of peripheral tissues 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 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 feet and tail, which proved to be the most labile in their temperatures, and were inversely correlated with the whole-body insulation.

At 30°C in air, high peripheral temperatures, due to vasodilation, accounted for increased heat dissipation (lowered whole-body insulation). This occurred when muskrats obtained a high thermal load, indicated by an elevated T_c. Such a situation may arise naturally due to high T_a, or increased metabolic heat production and storage during exercise. Indeed, free-living muskrats during the summer were observed to have deep body temperatures which increased during swimming and feeding activity (MacArthur, 1974). The body temperature in an adult male muskrat was reported to be usually over 39.0°C during activity. In this study, an observed mean T_c of 39.0°C was the point at which muskrats elicited vasodilation of the extremities. However, when muskrats were restrained at all T_a's in water, the T_c remained below 39°C and vasodilation was not observed. In fact at 20°C in water, T_c was maintained below normal. For all tests in water as with those at 20 and 25°C in air, heat conservation was maximized by maintaining a small thermal difference between the temperature of the appendicular skin and the environment.

Previous studies on muskrats have suggested the importance of regional heterothermy for control of thermal balance. Johansen (1961) found no peripheral warming at T_a ranging from 0 to 20°C in air, but at T_a's above 25°C the tail temperature rose to 35–37°C. In a later study, Johansen (1962a) showed tail blood flow during vasodilation to increase by a factor of more than 400. The increased tail blood flow was considered to be responsible for the prevention of heat accumulation in the body due to the high insulatory properties of the pelage. When the tail was immersed in ice water, tail skin temperature exhibited a rapid decline over 30°C–1°C. Johansen (1962a) believed that such a response reduced heat dissipation as indicated by the stability of the rectal temperature. Shcheglova (1964) reported steady increases in tail temperature of the muskrat in air and water as T_a increased from 0 to 35°C. However in the present study, appendicular temperatures were not observed to rise significantly above ambient except at 30°C in air.

Other studies illustrate the importance of heterothermic extremities for aquatic mammals. It was concluded that the naked tail of the beaver (*Castor fiber*) had a secondary function of controlling heat dissipation (Steen & Steen, 1965). 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 seal pups were submerged in water at 9°C T_a. The dorsal fin of 2 species of dolphin has also been shown to function both for heat conservation and dissipation (McGinnis *et al.*, 1972).

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 (SE) 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, the $\dot{V}_{O_2}$'s of McEwan *et al.* (1974) for unfasted and 24 hr fasted muskrats were exceeded by 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 animals. The $\dot{V}_{O_2}$ in water at 30°C for the present study was found to be comparable to Hart's (1962) data on muskrats for similar conditions. 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. The difference in the mean $\dot{V}_{O_2}$ between air and water in this study exceeded those 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. Such differences are probably due to the higher thermal conductivity of water compared to air.

Similarly, both the platypus, *Ornithorhychus 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 at thermoneutrality (Irving & Hart, 1957; Hart & Irving, 1959). Such differences in the metabolic responses of semi-

aquatic mammals may be due partly to differences in body size and to the effect of non-wettable fur versus blubber for insulation.

In water, insulation was found to decrease slightly as T_a increased, while a 42% reduction in whole-body insulation occurred between 25 and 30°C in air. Therefore the insulation was probably maximized in water, while in air the rapid decrease was produced by the increase peripheral warming augmenting heat loss. The higher thermal conductivity of water than air probably resulted in the lowered insulation in water. Morhardt *et al.* (1975) demonstrated that the rate of heat loss for non-aquatic birds and rodents immersed in water was 5–10 times as great as in air. Maximal values of whole-body insulation for muskrats were only 2.4 fold higher in air than in water at 25°C. The greater augmentation of heat loss from these non-aquatic animals, compared to the muskrat, would be expected due to the absence of specific adaptations of insulation to minimize the cooling effect of water.

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 reduce 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.

During testing, some 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 temperatures are equal to T_a. Although the heterothermic tissues of the extremity are 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 to occur. Circulation to the extremities could persist to allow for metabolic exchange while preventing undue heat loss by a counter-current heat exchanger.

Irving & Krog (1955) were first to propose the existence of a counter-current heat exchanger in the tail of the muskrat. They based their conclusions 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 exchangers were common in the tails of various rodents. Although Thorington did not study the tail of the muskrat, because of the commonality of heat exchangers in a variety of diverse rodents, it seems logical to assume that such a morphological system exists in the muskrat. Latex injections performed on the arterial and venous systems of the muskrat have shown a similar configuration of the vascular network to the arrangements in tails described by Thorington (1966). Of particular interest is the juxtaposition of arteries and veins. Three main caudal veins were found lateral to three caudal arteries and in direct contact with the arteries along the caudal vertebrate in the well insulated base of the tail. Conspicuous shunts occurred between the veins, while the arterial system was elaborate with numerous branches and shunts along the entire length of the tail. The femoral artery and vein, in the insulated portion of the hindleg, were found to break up into a complex of numerous smaller vessels in juxtaposition with one another. This anatomical evidence hints at the possibility of a counter-current exchanger in the muskrat tail and hindleg, although further morphological research is necessary.

In summary, it has been demonstrated that changes in the temperature of various body regions, especially the extremities, 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 limb 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 acquired thermal load. Such situations arise naturally due to high T_a, or increased metabolic heat production and storage during exercise. The higher thermal conductivity of water over air was surmised to be the causative factor in lower T_b's, decreased whole-body insulation, and increased $\dot{V}_{O_2}$'s for muskrats. In water the pelage and physiological insulation at T_a's below thermoneutrality were insufficient to prevent general body cooling. Conversely for the test T_a's in air, the pelage acted as an effective barrier to heat loss from the muskrat. It would appear, therefore that regional heterothermy 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 variable environments.

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