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THERMOREGULATION OF THE NORTH AMERICAN MINK DURING REST AND ACTIVITY IN THE AQUATIC ENVIRONMENT¹

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Thermoregulation during swimming and resting in water was investigated for the North American mink (*Mustela vison*, Schreber) in summer and winter pelage by measuring total heat production, heat storage, and minimum thermal conductance. Swimming activity over the range of $0.13\text{--}0.60\text{ m}\cdot\text{s}^{-1}$ resulted in heat losses that exceeded metabolic heat production within 5 min of immersion. This imbalance, manifested as a decline in core body temperature (core T_b), resulted in negative levels of heat storage. Negative heat storage for mink was greatest at intermediate swimming speeds. Maximum levels were $-14.28\text{ W}\cdot\text{kg}^{-1}$ at $0.29\text{ m}\cdot\text{s}^{-1}$ and $-8.72\text{ W}\cdot\text{kg}^{-1}$ at $0.36\text{ m}\cdot\text{s}^{-1}$ for mink in summer and winter pelage, respectively. Thermal conductance determined from cooling curves of carcasses and a taxidermic mount increased linearly with water speed and was comparatively greater at all speeds for animals in summer pelage. Patterns of cooling for carcasses, the taxidermic mount, and swimming mink were similar. In combination with regional heterothermy and elevated heat production, insulation provided by an air layer pervading the fur will permit short bouts of swimming in which T_b is maintained by foraging mink.

INTRODUCTION

Wild mink prey on a variety of animals that inhabit both aquatic and terrestrial environments. The selection of particular items varies with the season and presumably with prey availability (Gerell 1967). Pressures favoring the change from terrestrial to aquatic foraging include periods of increased difficulty of finding and capturing terrestrial food items and increased ease of hunting aquatic prey (Dunstone 1979). Aquatic activity by mink is not restricted to warmer months but is, in fact, increased during the winter. A study of wild mink in Sweden demonstrated that fish may account for $>50\%$ of the winter diet (Gerell 1967). Increased vulnerability of prey at lower water temperatures is believed to be

the causative factor. While fish exhibit decreased activity and agility, the mink, as a consequence of endothermic thermoregulatory mechanisms, suffers little or no apparent decrease in motor ability.

The present study examines the mechanisms of thermoregulatory control that permit mink to forage in the aquatic environment. Total heat production and storage, thermal conductance, and changes in body temperature while in water were investigated for animals at rest and during swimming over a range of speeds. Measurements were made using mink in both winter and summer pelage in order to determine the effects of seasonal changes in insulation on thermoregulation in the water.

MATERIAL AND METHODS

HEAT PRODUCTION

Two male (mean body weight = 1,236 g) and four female (mean body weight = 969 g) adult, ranch-bred mink were obtained from a local breeder. Guard hair length, underfur length, and pelt texture of these animals were similar to those of wild mink specimen pelts. Each mink was trained to swim against a current in a Plexiglas-and-wire cage positioned in the test section of a water flume. The animals swam at water speeds ranging from 0.13 to 0.70

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$\text{m} \cdot \text{s}^{-1}$. Ambient air was pulled into the cage at flow rates of 9–11 liters $\cdot \text{min}^{-1}$. Samples of exhalant air were pumped to an oxygen analyzer (S3-A; Applied Electrochemistry, Inc.) for determination of oxygen consumption ($\dot{V}\text{O}_2$) during swimming. All experiments were conducted in a temperature-controlled room and performed at an ambient temperature (T_a) of 21 C and a water temperature (T_{water}) of 20 C. Experiments were terminated if excessive struggling or diving behavior occurred. (For details of the water flume, the respirometry system, and calibration, see Williams [1983].)

Net swimming efficiency of mink is <1.8% at velocities <0.7 $\text{m} \cdot \text{s}^{-1}$ (Williams 1983). Therefore, as has been assumed for human swimmers (Nielsen and Davies 1976; Nadel 1977), useful external work during swimming is negligible, and $\dot{V}\text{O}_2$ is equivalent to heat production for the mink. Data for $\dot{V}\text{O}_2$ were converted to heat production assuming a caloric equivalent of 20.1 J/ml O_2 consumed (Bartholomew 1977).

T_b

Core T_b was measured continuously during rest in water and during swimming activity by radio transmitters (Minimitter, Inc.) implanted in two female mink. These data were used in the calculation of heat storage. Calibration and use of the transmitters are described in detail elsewhere (Williams 1981). In brief, calibrated transmitters were implanted into the peritoneal cavity of the animals. Following a 2-wk recovery period, systematic T_b measurements were made. Accuracy of the transmitters was periodically assessed by comparing Minimitter values to temperatures determined from a thermocouple inserted deep into the rectum. Over the experimental period transmitter values differed by <0.5–1.0 C from the thermocouple values.

Regional measurements of skin temperatures were made on five mink (two males, three females) anesthetized with a combined intraperitoneal injection of acepromazine/atropine/ketamine. To reduce possible thermoregulatory disturbances due to the anesthetic, minimum required doses were injected into quiescent animals. With the exception of one male, the dosages resulted in mild sedation characterized by a

reduction in motor coordination. Animals were suspended by fishnetting in the water tunnel and placed in body positions that resembled normal swimming postures (i.e., the head, neck, and dorsal surface of the animal remained above the water). Cutaneous temperature of the plantar surfaces of the left front and hind paws; proximal areas of the front and hind limbs; neck and tail regions; and middorsal and ventral trunk surfaces were measured by placing a 44-gauge copper-constantan thermocouple threaded into a 28-gauge hypodermic needle against the skin. Temperatures were displayed and recorded on a Hewlett-Packard logging multimeter (model no. 2467A), connected to a Bailey Bat-4 thermometer calibrated against a National Bureau of Standards precision thermometer. Core T_b was monitored simultaneously in these experiments using a thermocouple inserted ~ 3 cm into the rectum. The rectal probe was held in place by taping the lead to the animal's tail. Identical measurements were made on two anesthetized female mink in air. T_a averaged 23.8 C and T_{water} averaged 24.6 C during the experimental period.

THERMAL CONDUCTANCE

Whole body thermal conductance of mink in air and in water was determined by cooling-curve analysis of adult male and female mink carcasses and of a pelt-covered metal model of a female mink. Owing to the absence of behavioral and physiological influences, the values of thermal conductance obtained using this method are referred to as "minimum." This is to distinguish these values from thermal conductances calculated from the metabolic rates of live mink (see below). The techniques for carcass preparation are outlined in Morrison and Tietz (1957) and Calder (1969). Freshly killed adult mink were suspended by surgical twine either in air in an open-topped enclosure or in water within the test section of the flume. Care was taken to maintain the integrity of the pelt under both experimental conditions. During the course of cooling, T_b and T_a were monitored continuously with calibrated thermocouples connected to a Honeywell temperature recorder. Thermal conductance ($\text{W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$) was calculated from the product of the cooling constant and the specific heat of mammalian tissue (3.4

$\text{J} \cdot \text{g}^{-1} \cdot \text{C}^{-1}$; Hart 1951). Cooling constants for the carcasses and the model were determined from the slope of the $\log(T_b - T_a)$ versus time plot.

Construction of the taxidermic model was based on the procedure described by Bakken and Gates (1975). A skinned mink carcass was frozen in a natural swimming position and cast in dental-impression alginate (Jeltrate). Allowing half of the impression material to set before preparation of a second layer permitted the mink to be cast in halves. After removal of the carcass, impressions of the mink's right and left halves were obtained. Owing to the size of the mink, it was considered both unwieldy and costly to prepare a solid Wood's metal cast. Therefore, molten Wood's metal was spread over each half of the alginate impression to a thickness of ~ 1 cm. Following implantation of a 24-gauge copper-constantan thermocouple in the approximate center of the model, the two sides of the metal cast were sealed by melting Wood's metal along the seam with a soldering iron. The model was tested for leaks by placing it in a water bath. Holes and imperfections were corrected by lightly touching the surface with a hot soldering iron. The pelt retained from the frozen carcass was secured on the metal cast with cyanoacrylate adhesive. Air pockets were removed by smoothing down the pelt and gluing. On drying, the pelt conformed closely to the metal cast.

Thermal conductances of the mink model were determined from cooling curves generated by alternately warming and cooling the model. Cooling constants were multiplied by the specific heat of Wood's metal ($0.1474 \text{ J} \cdot \text{g}^{-1} \cdot \text{C}^{-1}$; Bakken and Gates 1975) and a calibration factor. The model calibration factor was obtained from the ratio of carcass to model thermal conductances. Prior to skinning, thermal conductance of the female mink carcass designated for the model was measured both in still air and in water. These values were compared to conductances measured for the model covered with the identical pelt and were used in the calibration factor calculation. Once measurements were completed for the model covered with winter pelage, the pelt was changed to that of a comparably sized female mink in summer pelage. In this way changes in minimum

dry conductance resulting from seasonal changes of the fur were determined. A calibration factor for summer pelage was determined as above. The advantage of the model lies in the ability to perform repeated measurements of conductance without (1) killing an inordinate number of animals, (2) problems related to carcass deterioration, and (3) differences in body size between individual animals.

Minimum conductance both in still and in moving water was determined by suspending the preheated metal model in the water tunnel by two loops of surgical twine. The model was placed in the water headfirst in order to simulate a dive. Care was taken to duplicate the natural swimming position of the mink and to avoid possible disruption of the air layer of the fur. Measurements were made at speeds comparable to the natural range of speeds exhibited by swimming mink. The drop in core T_b of the model was recorded continuously, as in the manner described above for calculation of minimum thermal conductance. Duplicate measurements were made of the model when covered by a winter pelt and when covered by a summer female pelt.

Mass-specific "dry" conductance (excluding evaporative water loss) of live mink during swimming activity was calculated from the following equation: conductance ($\text{W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$) = [Heat produced ($\text{W} \cdot \text{kg}^{-1}$) - Heat storage ($\text{W} \cdot \text{kg}^{-1}$)] / [$T_{\text{eff}}(\text{C}) - T_{\text{water}}(\text{C})$] for female mink in summer and winter pelage. T_{eff} represents the "effective" temperature for heat transfer of the mink and was calculated from the mean of T_{neck} , $T_{\text{dorsal trunk}}$, and $T_{\text{ventral trunk}}$ determined from regional heterothermy experiments in still water. Heat loss by evaporation was assumed to be negligible owing to the high relative humidity of the ambient air. Because heat transfer across the body surface is not uniform (Bakken 1976) and because accurate values for surface area are difficult to determine, conductance is presented on a per gram basis rather than in terms of per square centimeter of body surface.

RESULTS

HEAT PRODUCTION

Mean \pm SD heat production during quiet floating in still water was $6.08 \pm 0.39 \text{ W} \cdot \text{kg}^{-1}$ and $6.81 \pm 0.45 \text{ W} \cdot \text{kg}^{-1}$ for male

and female mink, respectively. No change in resting heat production occurred in the male with increases in water speed up to $0.54 \text{ m} \cdot \text{s}^{-1}$, and only a slight upward trend was observed for the female (fig. 1). The levels of heat production for mink resting in water at $T_{\text{water}} = 21 \text{ C}$ was approximately two times basal metabolic heat production in air (Farrel and Wood 1968; Iverson 1972).

Over the range of 0.13 to $0.70 \text{ m} \cdot \text{s}^{-1}$, steady-state heat production of swimming mink increased curvilinearly from 19.70 to $31.49 \text{ W} \cdot \text{kg}^{-1}$. Such a nonlinear relationship was anticipated owing to the influence of hydrodynamic factors on metabolism of swimming animals. For further details see Williams (1983). Data for male animals were indistinguishable from the data for female animals. Thirteen heat-production measurements of mink swimming in full winter pelage were similar to heat-production measurements of mink in summer pelage.

T_b AND HEAT STORAGE

Core T_b of mink in water was a function of both swimming speed and the duration of immersion. During quiet resting in water at $T_{\text{water}} = 21 \text{ C}$, T_b of female mink remained stable for 4–5 min, subsequently decreasing with time (fig. 2A). Swimming activity of mink in both winter and summer pelage resulted in a slight increase in T_b , followed by a continuous decline in T_b with time. The duration of the rising phase and the rate of body cooling were dependent on swimming speed. As in the case of the resting mink, high-speed swimming ($>0.40 \text{ m} \cdot \text{s}^{-1}$) was associated with rising phases of 4–5 min and gradual declines in T_b (fig. 2B). At intermediate swimming speeds ($\sim 0.30 \text{ m} \cdot \text{s}^{-1}$), T_b decreased following a 2–3-min rising phase (fig. 2A). A comparatively greater rate of T_b cooling was observed at these intermediate speeds.

Since it is a measure of the decrease in the total heat content of the body, the rate at which T_b decreased represents negative heat storage. This negative storage was determined from the slope of the relationship between immersion time and T_b during the declining phase. Data were separated into low- and high-speed fractions. Negative heat storage in summer and winter female

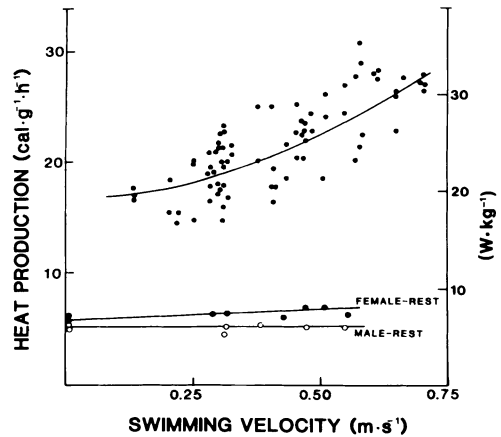


FIG. 1.—Mass-specific heat production for mink in relation to swimming velocity. Each point represents a single swimming bout for a single animal. Horizontal lines along the bottom of the graph represent values for male and female mink resting in water at various flow speeds. Solid lines through the data points are the best-fit regressions.

mink was greatest at intermediate swimming speeds and declined as upper and lower extremes in speed were approached (figs. 3, 4). Mean \pm SD values for female mink in summer pelage resting in water averaged $-5.91 \pm 1.54 \text{ W} \cdot \text{kg}^{-1}$ and increased with swimming velocity to $-11.49 \text{ W} \cdot \text{kg}^{-1}$ at $0.30 \text{ m} \cdot \text{s}^{-1}$. The highest level of negative storage measured was $-14.28 \text{ W} \cdot \text{kg}^{-1}$, occurring at a swimming speed of $0.29 \text{ m} \cdot \text{s}^{-1}$. With further increases in swimming speed, negative heat storage decreased in summer-furred mink (fig. 3).

The relationship between negative storage and swimming speed was qualitatively similar for winter- and summer-furred animals. However, the magnitude of negative heat storage was substantially reduced in mink with winter pelage (fig. 4). Resting negative heat storage for winter-furred females was $-1.50 \text{ W} \cdot \text{kg}^{-1}$, one-fourth of the summer value. The highest negative storage for females in winter pelage, $-8.72 \text{ W} \cdot \text{kg}^{-1}$, occurred at $0.36 \text{ m} \cdot \text{s}^{-1}$ and was 39% lower than the peak value for the female in summer pelage. At speeds $>0.36 \text{ m} \cdot \text{s}^{-1}$ negative heat storage of the winter-furred mink decreased with swimming velocity to levels lower than resting values. One mink in winter pelage forced to swim at $0.81 \text{ m} \cdot \text{s}^{-1}$ exhibited a consistent increase in T_b with time, and positive heat storage (fig. 4).

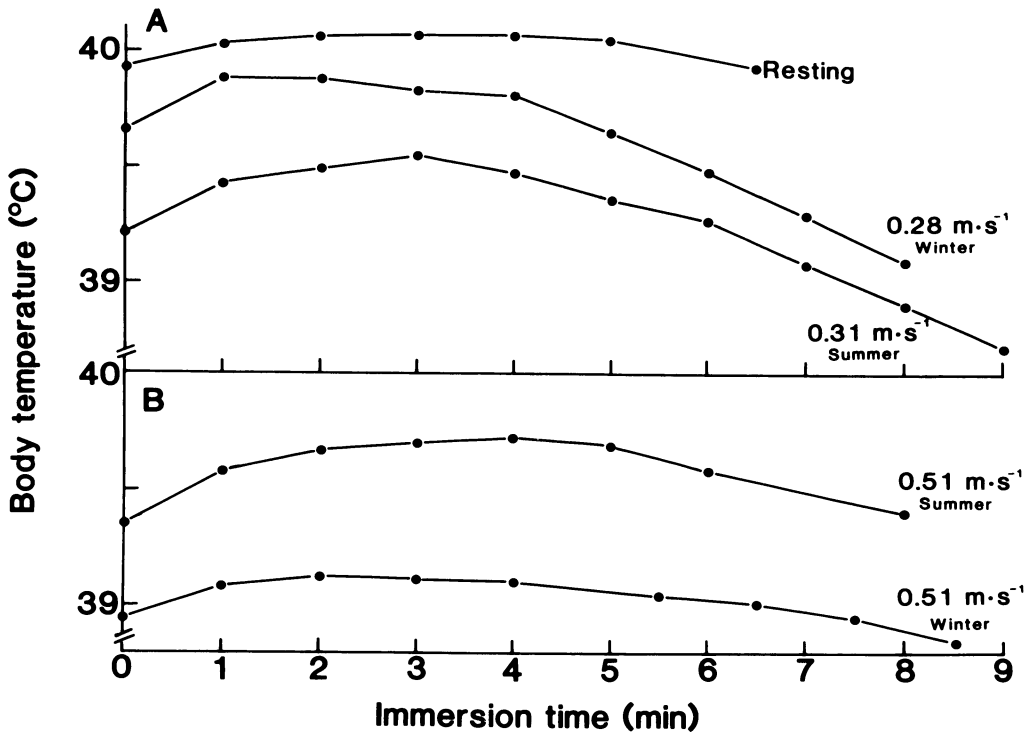


FIG. 2.—Core body temperature vs. immersion time for a female mink in summer and in winter pelage. Three different performance levels are illustrated, resting and intermediate speed swimming (A), and high-speed swimming (B).

REGIONAL HETEROTHERMY

Mean skin temperatures of eight different anatomical sites of anesthetized mink in

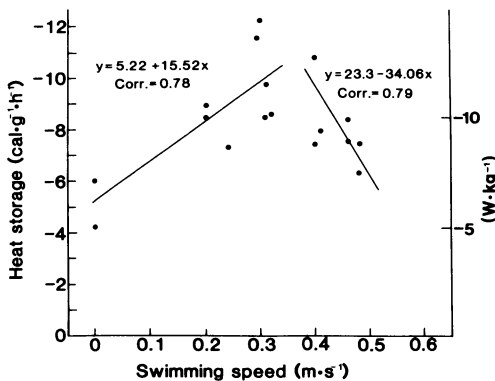


FIG. 3.—Negative heat storage in relation to swimming speed for two female mink in summer pelage. Solid lines represent the least-squares regressions through the data points. The data were subdivided into low- and high-speed fractions, and regressions with the highest correlation coefficients are presented. The intersection of the two regressions is used to represent the "peak" negative storage. Regressions present heat storage in $\text{cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ and are converted to negative heat storage by multiplying by -1.0 .

summer pelage at $T_a = 23.8^\circ\text{C}$ were within 10% of the mean core T_b (fig. 5A). The lowest mean skin temperature measured in air, 36.4°C , occurred on the tail. In contrast, mean skin temperatures of male and female mink resting in water showed marked variability. Mean rectal T_b was 3.3°C less than that measured in air for animals resting 12 min in water at $T_{\text{water}} = 24.6^\circ\text{C}$. All measured skin temperatures were less in water than in air, particularly for the front- and back-paw plantar surfaces. For example, the

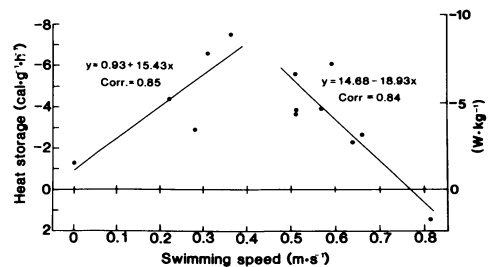


FIG. 4.—Negative heat storage in relation to swimming speed for two female mink in winter pelage. Legend is as for fig. 3.

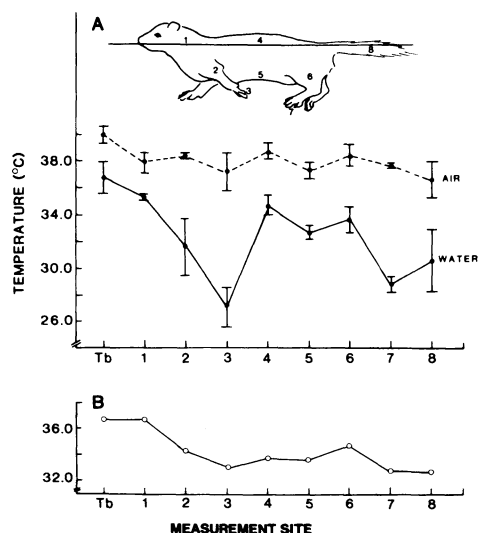


FIG. 5.—A, Rectal and cutaneous temperatures of anesthetized mink in summer pelage in air (● --- ●, $n = 2$), or in water (● — ●, $n = 3$) for approximately 10 min. Each point represents a mean value, and the vertical bars represent ± 1 SD. The profile illustrates the measurement sites with corresponding numbers on the ordinate. Note that the neck and mid-dorsal trunk (sites 1 and 4) were above the water level for the animals resting in water. B, Rectal and cutaneous temperatures of a heavily sedated male mink resting in water.

temperature of the front paw of the mink in water was 27.0 ± 1.56 C, 10.2 C less than the comparable value for mink resting in air, although T_a and T_{water} differed by less than 0.8 C.

Cutaneous temperature measurements of a heavily sedated (characterized by total loss of motor coordination) male mink resting in water demonstrated a different temperature profile (fig. 5B). As observed for other immersed mink, rectal and skin temperatures were less than the corresponding values for animals resting in air. However, the same pattern of regional heterothermy was not apparent for this animal. While most regional skin temperatures differed by less than 3%–8.5% from the mean values for other mink resting in water, temperatures of the plantar surfaces of the front and back paws were 22.2% and 14.1% greater than the respective means for immersed minks. As a result, T_b decreased at a rate of 0.25 C/min for this mink in comparison to a mean rate of 0.13 C/min for the other mink resting in water.

THERMAL CONDUCTANCE

Cooling curves of winter-furred mink carcasses in still and moving water were biphasic (fig. 6). Unlike monophasic cooling curves observed for still-air measurements, T_b of cooling carcasses in water showed a greater rate of decline following 2 min of immersion. Owing to the method of measurement, it was not possible to determine whether a relationship between the duration of this "precooling" period and the speed of water exists.

The importance of the insulating air layer in the fur was assessed by lightly rubbing two carcasses with a detergent solution. Prior to immersion the carcasses were rinsed in hot water. This procedure resulted in saturation of the pelt on immersion in the cooling tank. As illustrated in figure 6D, the detergent application abolished the precooling period in still water. The biphasic cooling pattern was reestablished in subsequent tests following drying of the pelt.

Cooling curves of the female model covered in winter pelage also demonstrated a biphasic pattern. Minimum thermal conductances during the first minute of immersion were significantly lower (at $P < .05$) than conductances calculated from the remainder of the curve (fig. 7). This was observed for both still- and moving-water measurements over the range of 0.32 – 0.97 $\text{m} \cdot \text{s}^{-1}$. Mean \pm SD minimum thermal conductance of the winter-furred model in still water was 1.44 ± 0.22 $\text{W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$ for the first minute and 1.76 ± 0.04 $\text{W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$ following more than 2 min of immersion. The respective means \pm SDs for 10 tests in moving water were 2.28 ± 0.32 $\text{W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$ and 2.85 ± 0.52 $\text{W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$. Although biphasic functions were also observed for a number of water velocities for the model covered by a summer pelt, the pattern was inconsistent. Therefore, similar conclusions cannot currently be drawn for mink in summer pelage.

Minimum thermal conductance of the adult male and female mink were determined from the portion of the cooling curve following the precooling phase, using carcasses and a taxidermic mount. Data for winter and summer pelage, in air and water, are compared in table 1. Entrance into the water resulted in a 7-fold increase in min-

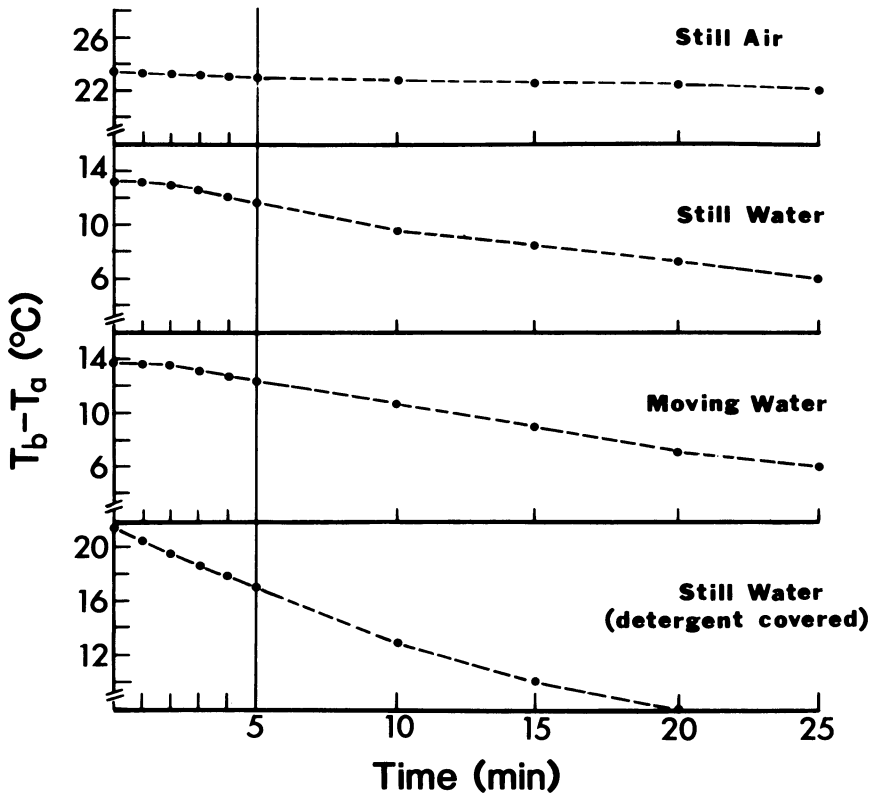


FIG. 6.—Representative cooling curves of a mink carcass in winter pelage. Note the 2-min precooling plateau present for both still- and moving-water measurements. This plateau was not observed for cooling curves determined either in still air or in still water following a detergent rubdown of the fur.

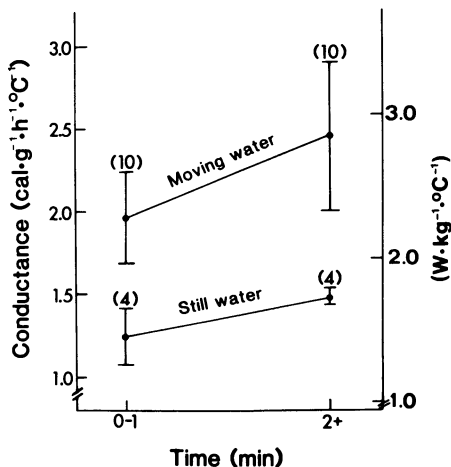


FIG. 7.—Minimum thermal conductance of a taxidermic mount covered in a winter mink pelt. Values are calculated for the first minute of immersion and for the remainder of the cooling curve. The mean thermal conductances determined for still and moving water were significantly different ($P < .05$) for each time period. Points and vertical bars represent the mean values ± 1 SD. Bracketed numbers represent n for each condition.

imum conductance for the winter-furred female, a 7.9-fold increase in minimum conductance for the winter-furred male, and a 5.4-fold increase for the summer-furred female compared to levels measured in air. Values for the female mink in summer pelage were 37% higher in still air and 5% higher in still water than those for the female in winter pelage. As a consequence of a comparatively lower surface-to-volume ratio associated with larger mass, winter-furred male mink demonstrated minimum thermal conductances that were lower than the female values, both in air and in water.

Over the range of 0–0.97 m·s⁻¹ minimum conductance of the winter female mink model increased with water speed (fig. 8) and is described by the following equation: minimum thermal conductance ($W \cdot kg^{-1} \cdot ^\circ C^{-1}$) = $1.90 + 1.43$ [water velocity (m·s⁻¹)] ($r^2 = .59$, $n = 16$). Summer females demonstrated a comparatively greater increase in minimum conductance with water speed. The equation for this re-

TABLE 1

MEAN \pm SD MINIMUM THERMAL CONDUCTANCE OF MINK IN STILL AIR AND WATER

MINK TYPE	THERMAL CONDUCTANCE (<i>n</i>) (W · kg ⁻¹ · °C ⁻¹)			
	Winter		Summer	
	Air	Water	Air	Water
Female carcass251 \pm .042 (5)	1.76 \pm 0 (2)
Corrected model249 \pm .005 (4)	1.76 \pm .041 (4)	.342 \pm .030 (6)	1.85 \pm .163 (3)
Male carcass205 \pm .021 (5)	1.62 \pm .064 (2)

lationship is as follows: minimum thermal conductance (W · kg⁻¹ · h⁻¹ · °C⁻¹) = 2.13 + 3.78 [water velocity (m · s⁻¹)] (*r*² = .72, *n* = 9).

Thermal conductance calculated from metabolic data for animals resting in water was 0.976 W · kg⁻¹ · °C⁻¹ for the summer females and 0.598 W · kg⁻¹ · °C⁻¹ for the win-

ter females. Swimming at 0.10 m · s⁻¹ resulted in a greater than 2.2-fold increase in conductance over resting levels for all of the females (fig. 9). While conductance increased with speed up to 0.4 m · s⁻¹, little change was observed with further increases in speed up to 0.6 m · s⁻¹. Thermal conductances for swimming mink in summer

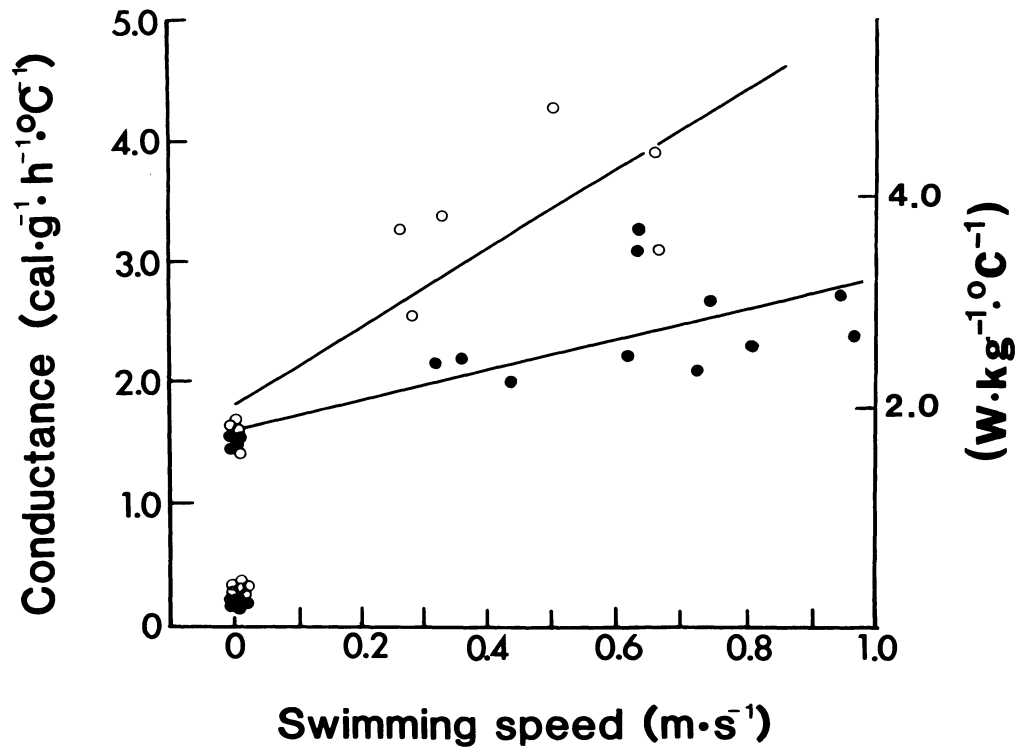


FIG. 8.—Minimum thermal conductance vs. water speed of a pelt-covered model. ● = data for a winter female pelt; ○ = data for a summer female pelt. Lines are fitted by the least-squares method and include data for conductances measured in still water. Equations and statistics are as given in the text. Grouped points at 0 speed in the lower portion of the graph are values for minimum conductance measured in air.

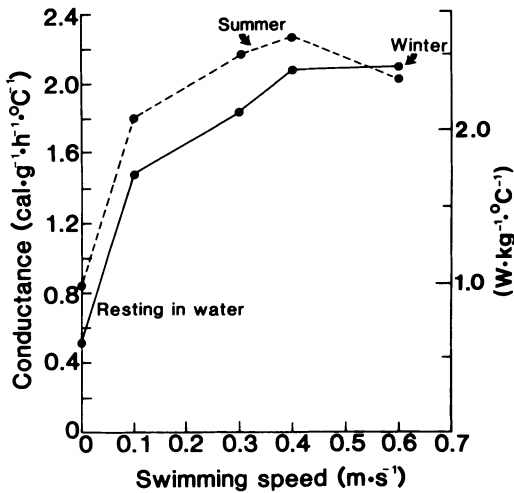


FIG. 9.—Thermal conductance, as determined from the metabolic data of swimming female mink, in relation to speed, ●—● = winter data, and ●---● = data for mink in summer pelage. Levels at the Y-intercept are for mink resting in water.

pelage were 9.3%–21.5% higher than those calculated for winter-furred mink over the range of 0.10–0.40 m·s⁻¹.

DISCUSSION

In many instances aquatic activity by mink results in levels of heat loss that ex-

ceed metabolic heat production within 5 min of immersion (fig. 10). Manifested as a reduction in core T_b (fig. 2), the imbalance between heat loss and production results in negative levels of heat storage (figs. 3, 4). This imbalance persists regardless of activity level or seasonal changes in pelage and is similar to thermal responses of other semiaquatic mammals (Johansen 1962; Calder 1969; Fanning and Dawson 1980), despite the large surface-to-volume ratio of the elongate mink.

The increase in minimum thermal conductance on immersion is less for mink than increases reported for pelts of a variety of semiaquatic mammals. Thermal conductance of mink carcasses in winter pelage was 7–7.9 times higher in still water than in still air (table 1). In comparison, Scholander et al. (1950) observed approximately 20–25-fold and 10-fold increases in minimum conductance of submerged pelts over still-air values for the winter pelage of polar bears and beavers, respectively. While it is tempting to conclude that mink fur is a superior insulator in water, the discrepancy between the latter values and those for the mink may be related in part to differences in the method of conductance determina-

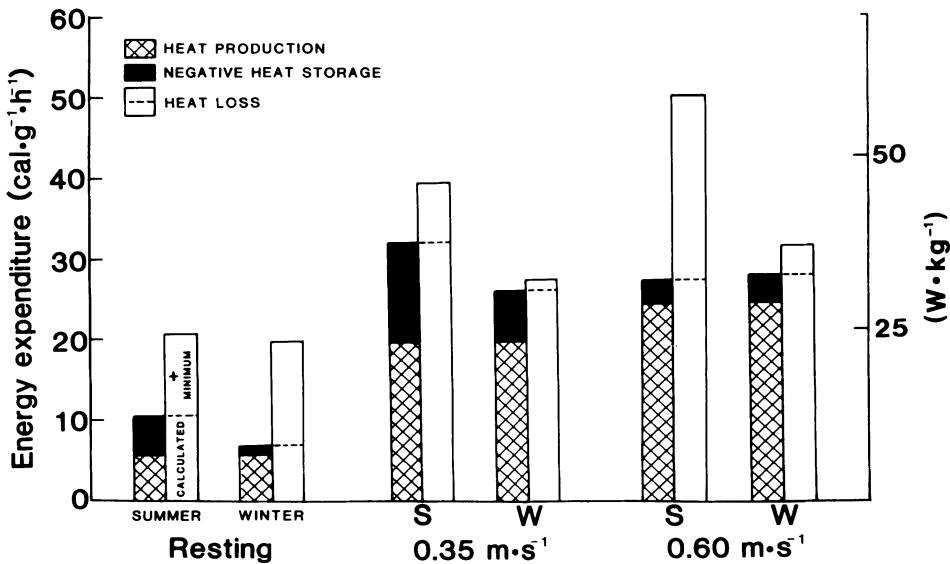


FIG. 10.—Mass-specific heat production, heat storage, and heat loss for female mink in summer and winter pelage. Three performance levels are presented. Heat production and heat storage are equivalent to calculated heat losses, represented by the area of the clear box under the dashed line. Thermal conductance determined by cooling-curve analysis was used to calculate "minimum" levels of heat loss and are represented by the entire clear boxes. Note that heat losses determined from cooling curves consistently exceeded levels calculated from metabolic data.

tion. Because whole mink carcasses were used, the conductance of the tissues and fat, as well as of the fur, influenced the level of heat loss measured. Subcutaneous fat, in particular, may provide a localized insulatory function in mink during locomotion, since it is deposited in areas most prone to fur disruption by swimming movements (Williams 1981).

The value of mink pelage as an insulator in water is dependent on the integrity of the air layer that pervades the fur on immersion. Retention of the air layer during the first minutes of immersion of a heated carcass or taxidermic mount most likely contributed to a comparatively lower rate of body cooling—and therefore to a lower minimum thermal conductance—in still and in moving water (figs. 6, 7). In comparison with pelts with the air layer intact, complete removal of the air layer elevated the rate of cooling in still water of female carcasses in winter pelage (fig. 6). The mean \pm SD minimum thermal conductance of the water-soaked model in still water averaged $2.81 \pm 0.313 \text{ W} \cdot \text{kg}^{-1} \cdot \text{C}^{-1}$ ($n = 2$), almost two times the minimum thermal conductance determined under the same conditions with an air layer present.

Similar results have been demonstrated for many semiaquatic mammals and for marine birds and mammals. Dawson and Fanning (1981) working on Australian water rats, Kooyman et al. (1976) looking at Adélie penguins, and Morrison, Rosenmann, and Estes (1974) investigating sea otters have all reported elevated thermal conductances associated with water infiltration of pelts in comparison with the unsaturated pelts of these animals. The effect of pelt saturation on thermal conductance varies with the animal and methodology. Ratios of saturated to control values measured in water ranged from two, for water shrews and mink carcasses, to seven, for live sea otters. Mechanical disruption or removal of the air layer also resulted in increased rates of heat loss in immersed, anesthetized muskrats (Johansen 1962) and in a decline in insulation of platypus (Grant and Dawson 1978).

Unlike other forms of insulation, an air layer pervading the fur is tenuous at best. Activities such as swimming and diving are particularly disruptive and often result in a

trail of air bubbles originating from the pelts (Tarasoff 1974; Kooyman et al. 1976). It follows that morphological adaptations that aid in retaining the air layer will increase the effectiveness of the fur in retarding heat loss in water. Specialized surfaces have been reported for the hair shafts of two semiaquatic mustelids, the river otter and the sea otter (Sokolov 1962; Tarasoff 1974). Cuticular scales cause individual hairs to interlock and entrap an insulating layer of air on submersion. It has been suggested by Sokolov (1962) that links in the wool hairs of some semiaquatic mammals increase hair resilience and prevent compression of the air layer during submerged swimming. It is likely that such a function is performed by the dense underfur of the winter mink pelt. A lack of density causes the summer coat of the mink to look "flat" (Kaszowski, Rust, and Shackelford 1970). Such pelage appears unable to retain a large air layer in water, particularly if the hairs are disturbed. Since winter mink pelage exhibits greater insulatory properties over a range of water speeds than does the summer pelt (fig. 8), it may have a greater capacity for the retention of the air layer, especially in moving water.

The unusual relationship observed between the T_b of live mink and the duration of swimming effort reflects the gradual decay of the air layer when the animal is swimming or resting in water (fig. 2). Like the precooling and cooling phases of the immersed carcass, core T_b 's of live mink characteristically rose, plateaued, and then declined steadily as exposure or performance progressed. It is speculated that the rise in T_b during the first minutes in water represents non-steady-state conditions in which (1) thermal gradients redistribute and (2) physiological responses, such as heat production and peripheral vasoconstriction, are initiated. Once a steady exercise state is reached, a reduction in the air layer—and concomitant increase in thermal conductance—will result in both the observed decrease in core T_b and the negative heat storage values.

As reported for humans (Nadel et al. 1974) and the Australian water rat (Fanning and Dawson 1980), changes in core T_b of mink are dependent on the level of swimming activity. However, the changes in heat

storage are not simply a function of increased heat loss with increased swimming speed. Rather, it appears to be a complex balance of increased heat production, decreased insulatory quality of the fur, and changes in peripheral vasoconstriction associated with increased swimming speed. Over the range of speeds investigated, the most thermally stressful situations—and therefore those that resulted in the greatest levels of negative heat storage for mink—occurred at intermediate swimming speeds (fig. 10). Likewise, Dawson and Fanning (1981) have reported that core T_b 's of water rats are highest when the latter are resting in water and at peak activity. Quiet swimming was associated with a decline in the core T_b 's of these semiaquatic rodents.

Physiological responses of live mink that are absent in the carcass and model have an important bearing on heat losses to the water. Total heat loss of mink in water, as calculated from minimum conductances of carcasses and a taxidermic mount (assuming an effective body surface temperature in water of 34.2 C) (table 1), consistently exceeded the total heat loss, as determined from metabolic data, of live mink (fig. 10). The discrepancy is attributed primarily to vascular adjustments associated with peripheral heterothermy (fig. 5). As a result the effective temperature gradient for heat transfer was lower than that assumed in the above calculation using minimum conductances of carcasses and models. It is interesting to note that these results are in direct opposition to those of Korhonen, Harri, and Asikainen (1983). These investigators determined thermal conductance in air from both cooling curves and the metabolic data of raccoon dogs, polecats, and mink. In this earlier study cooling-curve values underestimated metabolic calculations. The comparatively low thermal conductance values obtained from cooling curves were attributed to the absence of (1) heat losses through evaporative pathways and (2) warm blood transfer from the body core to the periphery. Because heat loss via these pathways is probably reduced for swimming mink, the differences observed between the present study and that of Korhonen et al. (1983) may be expected.

Because the paws are the most thinly insulated surface of the mink, they provide

the most probable control site for heat transfer. Localized vasoconstriction in these areas inhibits heat loss to the air (Segal and Ignatov 1975) or to the water (present study) by decreasing the exchange between warm blood from the body core and cold blood from noninsulated sites. Although the response is not exclusive to either the mink or aquatic animals in general, specialized arrangements of vessels that have been observed in many marine and semi-aquatic mammals provide important sites of thermoregulatory control during immersion. Thermoregulatory roles have been assigned to the complex cardiovascular anatomy of the extremities of the platypus (Grant and Dawson 1978), the tail and hind limbs of the beaver (Cutright and McKean 1979), the hind flippers of two species of seals (Tarasoff and Fisher 1970), and the fins and flippers of porpoises (Scholander and Schevill 1955). Regional heterothermy responsible for altering heat transfer across the extremities during immersion has also been observed in the muskrat (Johansen 1962; Fish 1979) and the Australian water rat (Fanning and Dawson 1980).

The significance of regional heterothermy in reducing heat loss in the submerged mink is apparent when the rate of cooling in animals demonstrating peripheral vasoconstriction is compared to that in an animal in which the response is absent. When fine control of the peripheral circulation was lost, as occurred in the heavily sedated male mink resting in water, the skin temperature of the paws remained close to T_b (fig. 5B). Consequently, heat transfer across these areas was comparatively high for this mink, and it was reflected in core T_b 's. T_b of the heavily sedated mink decreased at a rate of 0.26 C/min in comparison with a mean rate of 0.13 C/min for two mink exhibiting peripheral vasoconstriction.

Currently, it is difficult to provide a more precise explanation for the patterns of thermal imbalance observed in submersed mink. Many factors beyond the scope of this study may also contribute to the mechanism by which mink thermoregulate during swimming. Details that need to be examined include (1) the conflicting thermal and locomotor demands placed on the peripheral vascular system during swimming,

(2) the effects of increased forced convection associated with stroking movements of the appendages, and (3) the influence of piloreceptor responses on the maintenance of the air layer pervading the fur. Furthermore, the thermal responses of mink in winter pelage swimming at seasonal winter temperatures remain to be investigated.

Thermoregulatory factors governing aquatic behavior of mink, as well as the conflicting demands of the aquatic and terrestrial environments, may be examined in view of the results of this study. Swimming activity of wild mink is generally limited to short periods and is associated with predatory or escape behaviors. Hunting for aquatic food items consists of location of the prey from an aerial vantage point and "rush" tactics (Seton 1929; Poole and Dunstone 1976). As a result, little ecological pressure exists for extensive morphological

or physiological specialization for thermoregulation in the water, especially for prolonged swimming bouts. The ability of the mink pelt to retain an insulating layer of air for limited periods coincides with the limited swimming bouts observed for wild mink. Retention of an air layer, elevated heat production, and decreased peripheral temperatures appear to be effective in maintaining the T_b of mink during the first few minutes of swimming. The absence of either exceptionally long fur or large fat deposits also provides two important benefits for active mink: first, problems associated with physically hindered terrestrial locomotion are circumvented and, second, reduced heat dissipation during high levels of terrestrial activity is avoided; thus, exploitation of both the aquatic and terrestrial environments is possible for mink.

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