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## LOCOMOTION IN THE NORTH AMERICAN MINK, A SEMI-AQUATIC MAMMAL.

### I. SWIMMING ENERGETICS AND BODY DRAG

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(Received 17 June 1982 — Accepted 11 October 1982)

#### SUMMARY

Oxygen consumption ( $V_{O_2}$ ) during surface swimming and total body drag were investigated in the North American mink, *Mustela vison* Schreber. Over the range of  $0.13$ – $0.70$   $m\ s^{-1}$ ,  $V_{O_2}$  increased curvilinearly with speed for minks swimming against a current in a water flume. Similarly, body drag of a mink carcass increased non-linearly with speed and was described by the equation,  $Drag = 1.24 \text{ velocity}^{1.82}$ . A streamlined body shape, characteristic of many mustelids, aided in reducing drag at high speeds. Net swimming efficiencies were comparatively low ( $< 1.8\%$ ) and were attributed to high levels of drag when on the water surface and the absence of appendage specialization for aquatic locomotion. This lack of specialization probably contributes to high energetic costs but enables the mink to forage in both the aquatic and terrestrial environments.

#### INTRODUCTION

The biomechanical demands of aquatic and terrestrial locomotion are vastly dissimilar, and are reflected in different energetic costs for swimming and running (Schmidt-Nielsen, 1972). To cope with these demands, divergent evolutionary trends in appendage specialization have occurred. Webbed appendages characteristic of many aquatic species enhance the surface area available for thrust generation during swimming. In contrast, paw surface area is generally reduced in high speed runners. Presumably, these adaptations contribute to locomotor efficiency and decreased transport costs in their respective environments.

In many semi-aquatic birds and mammals, terrestrial mobility has been found to correlate closely to the degree of aquatic specialization (Tarasoff, Bisailon, Pierard & Whitt, 1972; Pinshow, Fedak & Schmidt-Nielsen, 1977). With increased specialization of one locomotor mode, a subsequent reduction in locomotor agility of alternate modes occurs. As a result, foraging is preferentially limited to a single habitat or means of locomotion for many semi-aquatic animals, with alternate environments supporting the animals for less mobile functions.

The North American mink, *Mustela vison* Schreber, appears to combine the effectiveness of weasels on land, and otters in water. Regardless of the season, minks forage

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Key words: Swimming, body drag, mink.

in both aquatic and terrestrial environments (Gerell, 1969). Unlike other semi-aquatic mammals, minks lack specialized appendages for swimming locomotion. Surface area of the feet is relatively small and the toes are only slightly webbed. Small appendages prevent awkwardness during terrestrial locomotion, but undoubtedly affect the efficiency of propulsive thrust generation during swimming.

The purpose of this study was to examine the locomotory energetics of surface swimming in *M. vison*. The interdependence of drag and metabolic rate was determined by measuring total body drag and oxygen consumption over a similar range of water speeds. Because minks utilize both aquatic and terrestrial habitats when foraging, the energetic consequences of the dual role of the appendages were examined in relation to swimming performance. The effect of this dual role upon running performance and transport costs was also determined and is reported elsewhere (Williams, 1983).

## MATERIALS AND METHODS

### *Animals*

Six adult, ranch-bred minks, purchased as 2- to 5-month-old kits from a local breeder, were used in these experiments. Two males (mean body weight = 1236 g) and four females (mean body weight = 969 g) were caged individually in facilities maintained at 20–25 °C under natural photoperiod. Food and water were provided *ad libitum*. All animals followed similar training regimes, and were allowed periodic access to an open tank of water. Once a degree of swimming proficiency was achieved, the minks were taught to swim against a current in a water flume. Data collection was delayed until each animal maintained steady levels of performance for a minimum of 20 min over a range of swimming speeds.

### *The water flume*

Body drag and swimming metabolic studies were conducted in a water flume constructed from a 132 × 66 × 66 cm glass aquarium (Fig. 1). Water was circulated in a circular pathway using an electric variable speed trolling motor, and flow velocities measured using a calibrated current meter (Gurley, model # 625F). A series of tubes and wooden struts located in front of a test section aided in reducing turbulence and permitted fine control of the speed and direction of the water within this section. To insure consistent flow in the test section, profiles of the water flow through this area were made by placing the current meter in different locations. Macro-turbulence in the test section was periodically assessed by observation of flow patterns of neutrally buoyant particles and aerated water. Although turbulence was noticeable at the highest speeds of the trolling motor ( $> 0.90 \text{ ms}^{-1}$ ), little or no turbulence was apparent over the range of swimming speeds investigated.

The minks swam in a 53 × 40 × 13 cm Plexiglass and wire respiratory chamber designed to permit unrestricted surface swimming. The chamber was placed in the test section of the water flume. Water levels were maintained just below the slanted portion of the chamber roof, creating an airspace around the subject's head. Room air was drawn into this space at flow rates of 9–11 l min<sup>-1</sup> and exited a manifold located

Behind the animal's head. The location of the airspace at the front of the test section forced the animals to swim against the current and maintain a stationary forward position during the tests (Fig. 1).

#### Metabolic determinations

Oxygen consumption measurements were made at  $T_{\text{ambient}} = 21^{\circ}\text{C}$  and  $T_{\text{water}} = 20^{\circ}\text{C}$ . Expired air drawn from the respiratory chamber was pumped through Drierite and Ascarite columns, and a flowmeter (Matheson, #604). Flowmeters were calibrated against a Brooks Volumeter. No significant difference was found between flowmeter calibration curves determined prior to, and following experimentation. Samples of the dried,  $\text{CO}_2$ -free air were shunted to an oxygen analyser (Applied Electrochemistry, Inc. S3-A) for determination of %  $\text{O}_2$ . The  $\dot{V}_{\text{O}_2}$  calculations were made using equation 4B of Withers (1977) and corrected to STPD. The entire system was calibrated daily with dried analysed gas mixtures, and tested for leaks by infusion with pure  $\text{N}_2$  gas.

Swimming  $\dot{V}_{\text{O}_2}$  was measured as minks swam against a single current velocity for 10–20 min. Steady state readings of %  $\text{O}_2$  were taken between 5–15 min after the start of swimming. The mink was considered in a steady state if  $\dot{V}_{\text{O}_2}$  varied by less than 6% over at least a 5 min period. The experimental range of swimming speeds,  $0.13\text{--}0.70\text{ m s}^{-1}$ , was determined by the swimming ability of the mink. During the

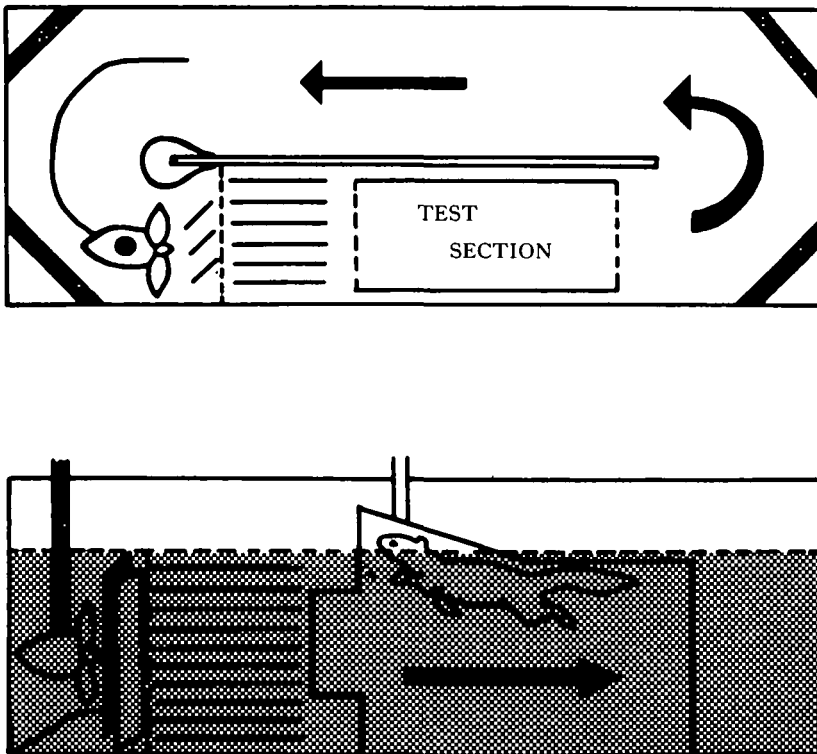


Fig. 1. Overhead and side views of the water flume used for the measurement of  $\dot{V}_{\text{O}_2}$  during surface swimming, and body drag. Arrows denote direction of water flow. The respiratory chamber illustrated in the side view was situated in the test section of the flume.

testing period an irregular schedule of speeds was established, with the animals performing only one swim on any test day.

During the training period two minks (one male, one female) initially refused to swim. When given access to the front screen of the respiratory chamber these animals floated passively on the water surface. Little movement of the limbs occurred with water speeds up to approximately  $0.55 \text{ m s}^{-1}$ . Steady state  $\dot{V}_{\text{O}_2}$  of these animals was used to represent resting metabolism in both still and moving water.

#### *Swimming mode and stroke rate*

Videotape recordings of swimming minks were made using a Sony Beta-Max video system. Frame-by-frame viewing of the tapes permitted swimming style, stroke length (as measured from the distal edge of the paws) and stroke frequency of the limbs to be determined. Representative swimming sequences were drawn from a television screen and still photographs.

#### *Drag*

Total body drag was determined using a mink carcass frozen in a natural swimming position. The carcass was attached to the lower vertical spoke of a freely rotating crossbar, and was positioned on the water surface in the water flume test section. Resistance created by the flow of water past the carcass displaced the crossbar. The original position was re-established by counterbalancing the resistive forces by the addition of known weights to a perpendicular crossbar spoke (See Webb, 1975). Fur characteristics, general body form, and relative position of surface swimming minks in the water flume were carefully reproduced. However, measurements of drag determined in this manner only approximate the drag of a swimming mink. Discrepancies in drag values between live animals and the frozen carcass may result from the rigidity of the carcass, and the influence of limb movements.

### RESULTS

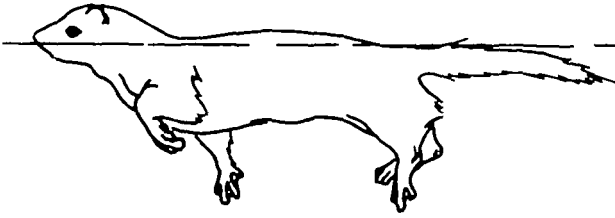
#### *Swimming mode*

The principal means of aquatic locomotion in the mink was an alternate thrust-recovery movement of all four limbs (Fig. 2). Initiation of the stroke occurred as the flexed limbs were moved anteriorly. The foot was compressed during this phase, thereby reducing resistance to movement. This was followed by full extension of the limb anteriorly and parallel to the horizontal axis of the body. Except during excited swimming or struggling, the paws remained below the water surface. Thrust was provided by moving the limb posteriorly. During the power phase of the stroke, the digits were spread, exposing maximal plantar surface area for propulsion. Termination of the stroke was followed by recompression of the digits. Flexion and anterior movement of the limb into the starting position completed the recovery phase and the stroke cycle.

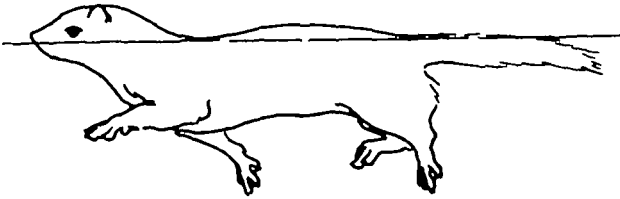
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Fig. 2. Swimming pattern of the mink. Note in particular, differences in extension of fore- and hind-paws, and synchronous movements of diagonal limbs.

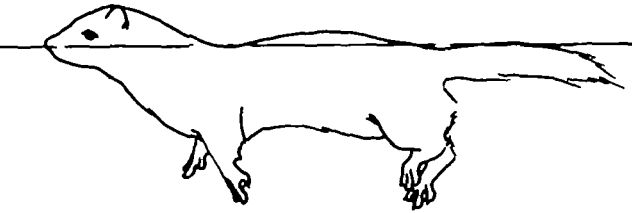
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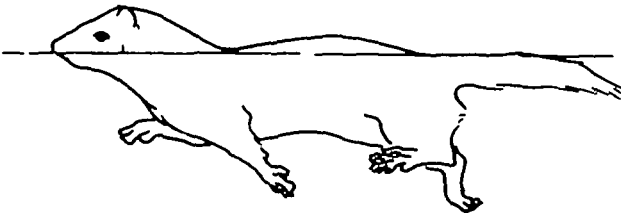
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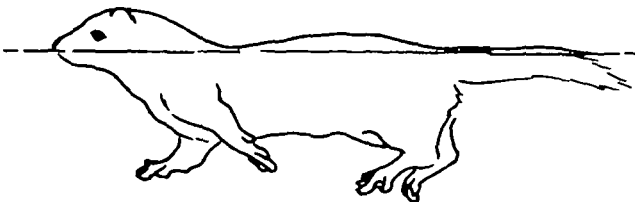


Fig. 2

Swimming was performed mainly by quadrupedal action with two diagonal legs moving in synchrony. The sequence was similar to terrestrial gaits used by the mink. Periodically, the hind limbs moved out of phase with the front limbs. This resulted in inconsistent limb movement sequences and brief periods in which lateral paws moved in synchrony. The major propulsive force for swimming was provided by the forepaws of the mink, and only secondarily by the hindpaws. This was evident from periods of passive hindpaw movement, particularly at low swimming speeds, and from qualitative differences in flexion and stroke length of the fore- and hindpaws (Fig. 2).

The minks generally floated horizontally in water with the head and part of the back exposed above the surface. A typical variation was a slight downward tilt of the caudal end with only the head exposed. The trunk of the body was held rigid during swimming. Undulatory movements of the body and tail, typical of many semi-aquatic swimmers, were not apparent over the speed range of  $0.13\text{--}0.70\text{ m s}^{-1}$ . Therefore, such movements appear to serve little if any propulsive function in minks.

#### *Stroke frequency*

Forepaw stroke frequency was independent of swimming speed at all velocities tested and averaged  $197.19 \pm 28.88$  (s.d.) strokes  $\text{min}^{-1}$  ( $N = 22$ ) (Fig. 3). Both fore- and hindpaw stroke frequencies were similar for individual animals, although differences in stroke length were apparent. A trend showing increased stroke frequency with decreasing body mass was observed. Mean forepaw stroke frequency for the largest mink (1570 g) was  $157.95 \pm 6.00$  strokes  $\text{min}^{-1}$  ( $N = 5$ ). The value for one of the smallest minks (1027 g) was  $230.10 \pm 15.36$  strokes  $\text{min}^{-1}$  ( $N = 5$ ) and was statistically different ( $P < 0.01$ ) from the larger animal.

#### *Metabolism and swimming speed*

Resting metabolic rates of minks floating in still water ( $\text{RMR}_w$ ) averaged  $1.09 \pm 0.07$  (s.d.)  $\text{mlO}_2\text{ g}^{-1}\text{ h}^{-1}$  ( $6.08 \pm 0.39\text{ W kg}^{-1}$ ) for the male, and  $1.22 \pm 0.08\text{ mlO}_2\text{ g}^{-1}\text{ h}^{-1}$  ( $6.81 \pm 0.45\text{ W kg}^{-1}$ ) for the female. Male  $\text{RMR}_w$  did not change with increases in water speed to  $0.54\text{ m s}^{-1}$ . Conversely,  $\text{RMR}_w$  for the female increased slightly with water speed, and at the highest speed ( $0.52\text{ m s}^{-1}$ ) was 20% greater than still water values (Fig. 4). The resting metabolic rate of these animals in water was almost twice basal values in air reported for minks by Farrell & Wood (1968), and Iverson (1972).

Steady state oxygen consumption ( $\dot{V}_{\text{O}_2}$ ) of swimming minks measured over the range of  $0.13\text{--}0.70\text{ m s}^{-1}$  increased with speed. Grouped data for the six minks fit equally well using both linear and power least squares regressions (Fig. 4). Based on regressions calculated for individual minks the grouped data is best described by the curvilinear function:

$$\dot{V}_{\text{O}_2} = 3.40 + 4.0 (\text{velocity})^{1.70}$$

where  $\dot{V}_{\text{O}_2}$  is in  $\text{mlO}_2\text{ g}^{-1}\text{ h}^{-1}$ , and velocity is in  $\text{m s}^{-1}$ . The 95% confidence interval for the scaling factor was 1.30–2.10.

$\dot{V}_{\text{O}_2}$  at the highest sustainable swimming speed was 4.8 times the mean  $\text{RMR}_w$  of the male and female minks floating at different water speeds, and approached t

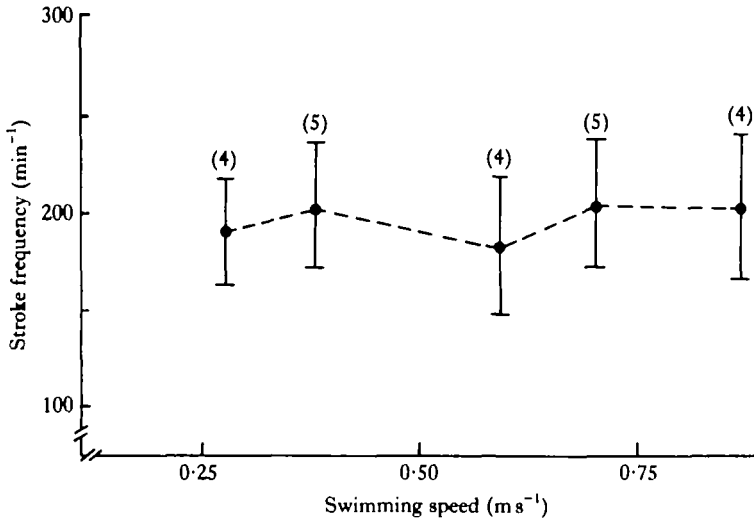


Fig. 3. Stroke frequency in relation to swimming speed in the mink. Each point represents the mean frequency for four or five different animals (as indicated). Vertical lines are  $\pm 1$  s.d.

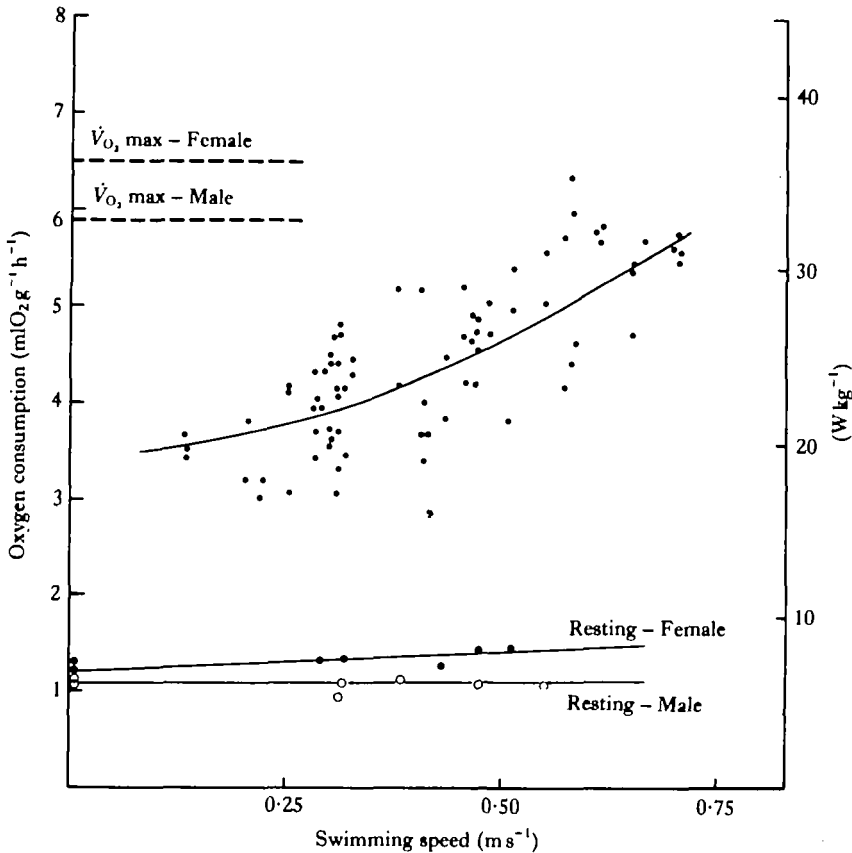


Fig. 4. Oxygen consumption plotted as a function of swimming speed for six minks. Solid circles midgraph represent single experimental swims for the animals. The solid line is the power regression through the data points ( $N = 75$ ,  $r = 0.70$ ). Plotted along the lower horizontal lines are values for minks resting in water at various flow speeds. Upper dashed horizontal lines denote maximum  $\dot{V}_{O_2}$  for minks, as determined during inclined treadmill running (Williams, 1983).



aerobic capacity of these animals. Female minks demonstrated a greater ability and willingness to swim at high speeds. The highest level of  $\dot{V}_{O_2}$  recorded during swimming was within 3% of the  $\dot{V}_{O_{2,max}}$  of  $6.50 \pm 0.41 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$  ( $36.27 \pm 2.29 \text{ W kg}^{-1}$ ), determined for female minks in an independent treadmill experiment (Williams, 1983). For male minks, the highest value of  $\dot{V}_{O_2}$  recorded during sustained surface swimming was approximately 14% below the measured maximum of  $5.90 \pm 0.27 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$  ( $32.92 \pm 1.51 \text{ W kg}^{-1}$ ).

#### *Drag and swimming efficiency*

Over the range of  $0.24\text{--}0.92 \text{ m s}^{-1}$ , total body drag of a frozen mink carcass on the water surface increased curvilinearly with water velocity (Fig. 5). The relationship is described as:

$$\text{Drag} = 1.24 \text{ velocity}^{1.82}$$

where drag is in newtons and velocity is in  $\text{m s}^{-1}$ . The 95% confidence interval for the scaling factor was  $1.72\text{--}1.92$ . Values for total body drag determined from this

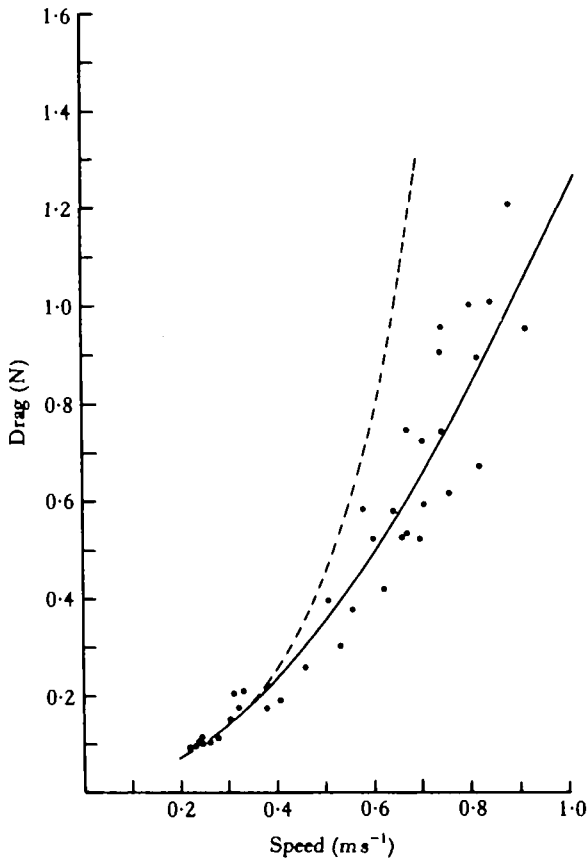


Fig. 5. Total body drag in relation to water speed for a mink carcass on the water surface. Each point represents a single drag experiment ( $N = 37$ ,  $r = 0.95$ ). The broken line is the relationship for drag vs water speed for a decoy duck (Calculated from Prange & Schmidt-Nielsen, 1970).

Relationship demonstrated a 22-fold increase over the experimental range of swimming speeds for the mink.

Mechanical power output ( $P_o$ ) of the swimming mink was estimated from the product of body drag and water velocity. Using the above relationship for the body drag of a mink carcass the resulting equation for  $P_o$  was:

$$P_o = 1.24 \text{ velocity}^{2.82}.$$

Total metabolic power input ( $P_i$ ) was calculated from swimming  $\dot{V}_{O_2}$  measurements. By taking the ratio of  $P_o$  to  $P_i$ , the percentage locomotor efficiency of swimming minks was determined. Net efficiency was also determined since minks, like many aquatic and semi-aquatic mammals, exhibit greater metabolic levels when resting in water than in air (i.e. – platypus, Grant & Dawson, 1978; muskrat, Fish, 1979). Because of this elevated metabolic rate, a disproportionate amount of the power input may serve no locomotor function. The net value was calculated from the ratio of  $P_o$  to  $P_{i,net}$ , where  $P_{i,net}$  was equivalent to the difference between total active and resting metabolic rates in water.

Locomotor efficiency of the minks was positively correlated with swimming speed (Table 1). Net swimming efficiency was 27–52% greater than total efficiency with the greatest improvement observed at the lower speeds.

## DISCUSSION

### *Body drag during swimming*

Physical properties of water and morphological characteristics of minks influence swimming performance by these animals. In contrast to terrestrial locomotion, in which air resistance generally contributes little towards opposing forward motion (Pugh, 1971), the viscous nature of water tends to retard locomotor movements. Resistive forces encountered by swimming animals consist of a complex combination of frictional drag, pressure drag and wave drag (Hoerner, 1965). The magnitude of each type of drag is determined by body size and shape, velocity of movement, the pattern of fluid flow around the body, as well as the viscosity and density of the fluid. Factors related to body shape in particular are important in reducing drag in minks.

Table 1. *Power input, power output and efficiency of swimming minks*

$\dot{V}_{O_2}$  ( $l h^{-1}$ ) was converted into metabolic power input (W) by assuming a caloric equivalent of 4.8 Kcal  $l O_2^{-1}$  of  $O_2$  consumed, and a conversion factor of 1.163 W  $Kcal^{-1} h^{-1}$ . Mechanical power output (W) was determined from the product of water speed ( $m s^{-1}$ ) and body drag (N).

Speed ( $m s^{-1}$ )	Drag (N)	$\dot{V}_{O_2}$ ( $l h^{-1}$ )		Mechanical power output (W)	Metabolic power input (W)		% Efficiency	
		Total	Net		Total	Net	Total	Net
0.15	0.039	3.64	2.42	0.006	20.32	13.50	0.029	0.044
0.20	0.066	3.74	2.52	0.013	20.87	14.06	0.063	0.092
0.30	0.139	4.01	2.79	0.042	22.38	15.57	0.188	0.270
0.40	0.234	4.34	3.12	0.094	24.22	17.41	0.388	0.540
0.50	0.351	4.73	3.51	0.176	26.39	19.59	0.667	0.898
0.60	0.489	5.19	3.97	0.293	28.96	22.15	1.01	1.32
0.70	0.648	5.71	4.49	0.454	31.86	25.05	1.43	1.81

Assuming that the mink's body approximates a streamlined hull shape, total frictional and pressure drag, calculated from conventional drag formulae (Shapiro, 1961) for a submerged male mink at the extremes of the range of swimming speeds, was 0.004 N at 0.15 m s<sup>-1</sup>, and 0.093 N at 0.70 m s<sup>-1</sup>. In contrast, experimentally determined drag for mink carcasses positioned on the water surface (Fig. 5) was seven to ten times greater than the calculated values for submerged animals. The discrepancy is partially attributed to the initiation of a surface wave system and, therefore, the addition of a wave drag component to total drag. Other potential sources of drag not accounted for in the submerged drag calculation are associated with the roughness of the mink's exterior, and projection of the limbs. The result is that the difference between these values for submerged and surface drag of minks is greater than the three- to five-fold difference reported for a body towed on and below the water surface (Hertel, 1966).

The swimming behaviour of minks, particularly at high swimming speeds, tends to reflect the differences in drag associated with submerged or surface performances. Surface swimming in the flume at velocities above 0.75 m s<sup>-1</sup> resulted in a build up of water directly in front of the animals. At these speeds prolonged surface swimming was avoided by interrupting surface bouts with increased periods of underwater swimming. Similarly, alternating periods of surface swimming and diving have been noted for wild minks (Seton, 1929). In the wild, submerged swimming has the added advantage of serving as an evasive manoeuvre during escape as well as subjecting the minks to reduced drag at high swimming speeds.

Over the lower range of speeds which supported sustained surface swimming by minks, total body drag increased curvilinearly with speed (Fig. 5). The non-linear relationship is characteristic of other bodies moving on the water surface. Exponential or curvilinear drag versus speed functions have been described for ships (Marchaj, 1964; cited in Prange & Schmidt-Nielsen, 1970), ducks (Prange & Schmidt-Nielsen, 1970), humans (Miyashita & Tsunoda, 1977), and muskrats (F. E. Fish, personal communication). Although the basic shape of the relationship is similar for these subjects, the relative magnitude varies greatly as a consequence of body morphology.

Morphological characteristics, such as body shape and surface projections, influence the pattern of fluid flow around a moving body and therefore, affect body drag. Because of a pressure gradient along the body, there is a tendency for the boundary layer to separate from the body surface downstream from the shoulder region (Shapiro, 1961). Vortices are formed, and a wake is produced as a consequence of this separation. The point at which separation occurs is a function of body shape (Fig. 6). Streamlined bodies, like the mink, experience reduced flow separation due to the movement of the separation point (s) closer to the tail. While a tapered body shape does not prevent turbulent boundary layer flow in minks (Mordvinov, 1974), delayed flow separation results in a smaller wake, less disturbance to flow, and reduced pressure drag (Webb, 1975).

The degree of tapering or, in other words, the streamlined quality of a body can be determined by the thickness ratio ( $T_r$ ), where

$$T_r = \frac{\text{maximum body diameter, } D}{\text{body length, } L}.$$

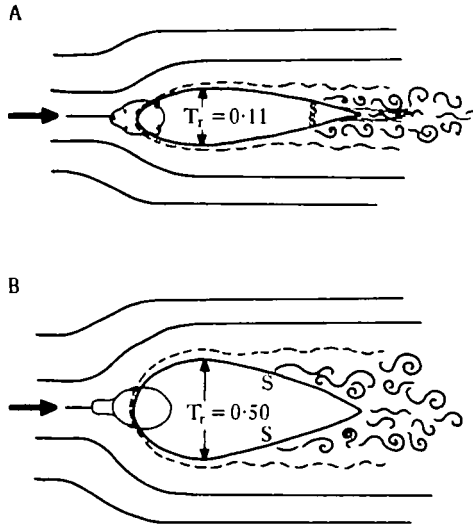


Fig. 6. Comparisons of thickness ratio ( $T_r$ ) and fluid flow around (A) a streamlined body as represented by the mink, and (B) a blunt body as represented by the duck. S denotes the relative point of flow separation for the boundary layer.

For a variety of streamlined swimmers, including aquatic mammals and large, fast swimming fishes,  $T_r$  ranges from 0.10 to approximately 0.24 (Hertel, 1966). Thickness ratios for minks fall within this range and average 0.11 (Fig. 6). In contrast,  $T_r$  for the blunt bodies of ducks are four to five times that of minks (personal observation).

The advantage of a low  $T_r$  for surface swimmers is demonstrated by comparing the body drag of minks and ducks of similar body mass (Fig. 5). At water speeds greater than  $0.40 \text{ m s}^{-1}$ , the drag of minks was consistently lower than reported for a decoy duck (Prange & Schmidt-Nielsen, 1970). The difference in drag for these animals increased with increasing water velocity, such that body drag was approximately 2.4 times greater for the duck at  $0.70 \text{ m s}^{-1}$ . Since body drag provides an estimate of the resistive forces encountered by the animal, it should be reflected in the energetic cost of swimming. Therefore, it is expected that body streamlining decreases the energetic demands of swimming locomotion by reducing drag.

#### *Swimming energetics, speed, and efficiency*

Swimming animals, as a consequence of hydrodynamic constraints, exhibit very different metabolic rates and energetic costs of transport compared to runners. A wide variety of mammals running on treadmills demonstrate nearly linear increases in oxygen consumption with running velocity (Taylor, Schmidt-Nielsen & Raab, 1970; Baudinette, Nagle & Scott, 1976). While linear increases in  $\dot{V}_{O_2}$  with speed have also been observed for swimming muskrats (Fish, 1982) and marine iguanas (Gleeson, 1979), many underwater and surface swimmers, including fish (Brett, 1964; Gordon, Loretz, Chow & Vojkovich, 1979), man (Holmer, 1972; Nadel *et al.* 1974), ducks (Prange & Schmidt-Nielsen, 1970), turtles (Prange, 1976), sea lions (Kruse, 1975), and minks (Fig. 4) show exponential or curvilinear increases in metabolism.

The rapid rise in metabolic rate with swimming speed for these subjects is attributed to the pronounced elevation in total body drag occurring with increasing velocities. As observed for ducks (Prange & Schmidt-Nielsen, 1970), changes in  $\dot{V}_{O_2}$  of swimming minks paralleled increases in body drag measured over a similar range of speeds. Like body drag, the rate of change in  $\dot{V}_{O_2}$  with swimming speed for the duck was greater than that measured for minks. For example, from 0.45 to 0.70  $\text{m s}^{-1}$ ,  $\dot{V}_{O_2}$  almost doubled for ducks and increased by only 26% for similarly sized minks. These different rates are most likely related to the effects of streamlining and body drag upon the swimming metabolism of these two subjects.

Drag associated with body position in or on the water also affects the energetic costs associated with swimming. This was demonstrated by Schmidt-Nielsen (1972) in a comparison of transport costs for surface and submerged swimmers. In minks, the minimum cost of transport of surface swimming was approximately 9.81  $\text{cal g}^{-1} \text{km}^{-1}$ , and was 19 times the predicted value for a fish of similar body mass (Brett, 1965). The high cost of swimming for minks, as for other surface swimmers, is partially due to energy wasted in the formation of surface waves and the influence of these waves upon total body drag.

Along with drag considerations, high swimming transport costs of minks is associated with an inefficient mechanism of thrust generation. The effectiveness of a limb in providing thrust to overcome drag is closely associated with locomotor efficiency in the water. Large, specialized surface areas for propulsion result in greater efficiency through an elevation in the amount of water moved per stroke, and a reduction in stroke frequency. Morphological trends in semi-aquatic mammals demonstrate hind limb specialization for increased surface area (Tarasoff *et al.* 1972). This is evident in the interdigital webbing characteristic of beavers, muskrats, otters and seals. The paws of minks have remained compact and relatively small in comparison to these semi-aquatic species. Based on the ratio of hindpaw propulsive surface area to total wetted surface area of the body, the effectiveness of the propelling system decreases in order from beaver, through muskrat, to mink (Mordvinov, 1976). Data from the present study indicates that the small propulsive surface area afforded by the paws of the mink may affect swimming efficiency. Despite an increase in net swimming efficiency over the range of speeds investigated (Table 1), the efficiency of minks was consistently lower than values reported for animals better adapted for the movement of water during a propulsive stroke (i.e., ducks, Prange & Schmidt-Nielsen, 1970; turtles, Prange, 1976). Comparable and even greater efficiencies have also been reported for the awkward efforts of men performing the front crawl (di Prampero, Pendergast, Wilson & Rennie, 1974; Rennie, Pendergast & di Prampero, 1975), although a unique method of drag determination for efficiency calculations was used in these studies.

Deficiencies, in terms of thrust generation, associated with low plantar surface area may be compensated by minks by long stroke lengths, high stroke frequencies, and by supplementation of forepaw propulsion by the hindpaws. A limitation in the range of stroke lengths afforded by the mink's enshortened limbs and the constancy of stroke frequency (Fig. 3) suggests that the latter plays an increasingly greater role at higher swimming speeds. In view of the low efficiencies observed for minks, such high stroke frequency, quadrupedal swimming is an energetically costly form of aquatic locomotion. Hindpaw movements used to supplement forepaw paddling potentia

interfere with the flow of water displaced during the forepaw power stroke. This seemingly inefficient mode of swimming was reflected in the cost of transport for minks. Minimum swimming costs of minks were not only much greater than predicted for fishes, but were also greater than reported for similarly sized surface swimmers having comparatively large propulsive surfaces (T. M. Williams, in preparation).

The success of the mink as a semi-aquatic animal should not be based upon swimming efficiency or cost of transport *per se*, but rather on the ability of the animal to exploit the aquatic environment when searching for prey. Observations of wild minks indicate that the driving force for food selection is the availability of prey (Gerell, 1967). The principal food groups represented in the mink diet, mammals, birds, fishes, and amphibians, suggest that the mink hunts in both aquatic and terrestrial habitats.

The unusual shape of the mink provides specific advantages in each environment. It has been suggested that an elongate body was originally evolved by mustelids as a predatory strategy enabling entrance into burrows in search of prey (Brown & Lasiewski, 1972; Gambaryan, 1974). However, this streamlined shape also provides a distinct advantage for high speed swimming by reducing total body drag and the consequent energetic demands. Since minks usually enter water either to escape predators or to hunt prey, characteristics which contribute to speed and agility rather than endurance are especially beneficial. This is particularly important during foraging underwater, where a limitation in oxygen availability may restrict the duration of prey pursuit (Dunstone & O'Connor, 1979).

In conclusion, surface swimming by the North American mink is an energetically expensive form of locomotion because of body drag and an inefficient mode of thrust generation. The absence of specialized surfaces for the propulsion of water during aquatic locomotion in conjunction with a quadrupedal paddling style of swimming undoubtedly contributes to the high locomotor costs observed for minks. However, preadaptation for speed in the water through body streamlining, and the maintenance of small paws for running, have resulted in the mink's ability to exploit both aquatic and terrestrial environments.

This work was carried out as part of a doctoral research project. It was supported by NSF grant PCM 8011158 to Timothy M. Casey. I am particularly grateful to Dr Casey for both his support and insights which proved invaluable to this study. I also thank Drs R. Barfield, M. L. May, C. R. Taylor, P. W. Webb and E. J. Zambraski as well as my new colleagues at Scripps for reading the manuscript and providing useful discussion.

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