

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

II. THE EFFECT OF AN ELONGATE BODY ON RUNNING ENERGETICS AND GAIT PATTERNS

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SUMMARY

Oxygen consumption (\dot{V}_{O_2}) of minks increased non-linearly with running speed over the range of 0.70–6.40 km h⁻¹. A break in the \dot{V}_{O_2} vs speed relationship occurred at approximately 3.94 km h⁻¹ and corresponded to the transition from a walking to a half-bounding gait pattern. Incremental transport costs associated with bounding were 36% lower than for walking at similar speeds. The lower energetic cost of bounding was attributed in part to low stride frequencies and in part to spinal flexion. The latter was particularly important in circumventing stride length restrictions associated with the short limbs of these animals. As a result, stride frequency and stride length of these elongate mustelids at the gait transition speed were similar to values predicted for conventionally-shaped mammals.

INTRODUCTION

Studies of terrestrial locomotion have covered a wide range of experimental subjects and have produced surprisingly consistent results. Despite various morphological and locomotor differences, many vertebrates demonstrate predictable energetic and mechanical patterns during running. For example, similar linear increases in oxygen consumption occur for bipeds and quadrupeds whether various similarly-sized animals (Fedak & Seeherman, 1979) or the same animal performing two- or four-legged running gaits (Taylor & Rowntree, 1973) are compared. Erect vs wide stances (Bakker, 1972) or the configuration of the mammalian limb with regards to centralization of the muscle mass (Taylor *et al.* 1974) also cause little if any deviation from predicted increases in running metabolism.

Two characteristics of mink (*Mustela vison* Schreber), that is, its atypical body morphology and semi-aquatic life style, lead one to suspect that the locomotor energetics of this species will not follow the normal mammalian pattern. Mink, with their elongate shape and short limbs, encounter problems of body support and restrictions in stride length not experienced by longer legged vertebrates. Furthermore, in order

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to forage in both aquatic and terrestrial environments (Gerell, 1967), minks require two very different modes of locomotion. Such demands are foreign to swimming or running specialists and would appear to require a compromise in morphological adaptations for locomotion by minks.

The purpose of this study was to examine the effect of an unusual body morphology upon terrestrial locomotion in the mink. Both mechanical and metabolic parameters were investigated through measurements of gait patterns, stride frequency and stride length, and oxygen consumption over a wide range of running speeds. Relationships between running energetics and gait characteristics were determined for minks. The energetic consequence of a bimodal locomotor system was examined by comparison of these data with predicted values for primarily terrestrial mammals.

MATERIALS AND METHODS

Oxygen consumption

Four adult female (mean body weight = 868 g), and one adult male (body weight = 1019 g) ranch-bred minks were trained to run in a Plexiglass chamber which slid on a treadmill belt. An open flow system of oxygen analysis was used with room air drawn in along the lower edge of the chamber at flow rates of approximately 10–16 l min⁻¹. Expired air exited at a port located on the top of the box and was drawn through a Drierite column and flowmeter. Flowmeters were calibrated against a Brooks Volu-meter. No significant difference was found between flowmeter calibration curves determined prior to and following experimentation. Samples of the dried, expired air were shunted to an oxygen analyser (Applied Electrochemistry, Inc., S3-A) for determination of % O₂. \dot{V}_{O_2} calculations were made using equation 3A of Withers (1977) and were corrected to STPD. The entire system was calibrated daily with dried analysed gas mixtures, and tested for leaks by infusion with pure N₂ gas.

All experiments were conducted at $T_a = 21^\circ\text{C}$. Each mink was placed in the chamber and allowed to rest for approximately 10 min. The treadmill was turned on to the desired speed, and % O₂ was monitored continuously. During the experiment, the minks maintained position at the front of the running chamber. The animals ran for 12–20 min and were considered to be in a steady state when \dot{V}_{O_2} varied by less than 4% over at least a 5 min period. Following the run, the animals were either returned to their cages or allowed to recover to resting \dot{V}_{O_2} levels before beginning a second experimental run. The range of running speeds was limited by the ability of the mink to keep up with the tread at high speeds, and by an inability to maintain a steady walking gait at the lower speeds. At velocities less than 3.0 km h⁻¹ the animals were tested at two different running speeds on a single day, while only a single experiment was conducted per animal per day at higher velocities. Experiments were terminated if running performance was inconsistent (i.e. – intermittent periods of turning, scratching, etc.). The treadmill was calibrated daily and an irregular schedule of test speeds used in order to preclude training effects.

\dot{V}_{O_2} max was measured using a modified procedure from Åstrand & Rodahl (1977). This consisted of running the animals at 4.5 km h⁻¹ and progressively increasing the work load by increasing the incline at which they were forced to run. Incline was

increased at rates of 2°min^{-1} , and \dot{V}_{O_2} was continuously measured until further increases in the slope of the treadmill did not result in a further increase in \dot{V}_{O_2} .

Stride characteristics

Films of running minks were made using a Sankyo Super 8 movie camera at a film speed of 36 frames s^{-1} . Gait patterns, stride frequency, and stride length were determined from the films using a Bell and Howell frame-by-frame projector. Representative gait sequences were photocopied from a microfilm viewing screen for analysis of footfall patterns.

RESULTS

Oxygen consumption

Oxygen consumption (\dot{V}_{O_2}) of minks exhibited two different linear functions with running speed (Fig. 1). A break in linearity of the \dot{V}_{O_2} vs running speed relationship was observed at approximately 4.0 km h^{-1} . The breakpoint was determined statistically by serial least squares linear regressions. Data points from the 'low speed' data set were progressively eliminated and were used to create a high speed data set. A least

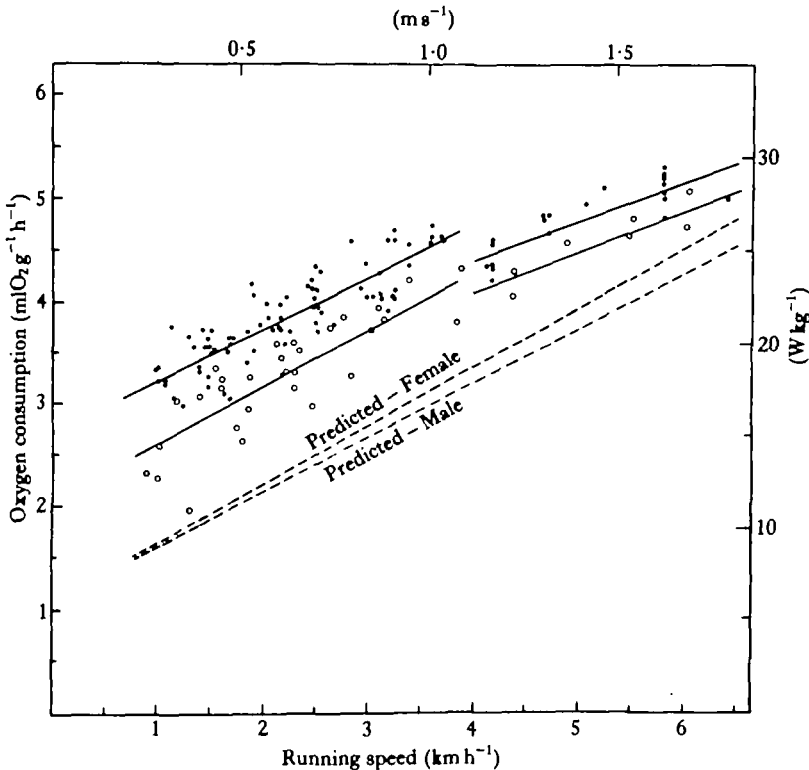


Fig. 1. \dot{V}_{O_2} plotted as a function of running speed for female (●) and male (○) minks. Each point is data for a single run for one animal. Solid lines denote least squares linear regressions through the data points. Dashed lines represent the predicted relationships for mammals of comparable body size from Taylor *et al.* (1982).

squares test was run with each elimination and regressions with the highest correlation coefficients for the 'high' and 'low' speed data sets used to explain the distribution of the data. The difference between the slopes of these data sets was statistically significant at the $P < 0.001$ level for both male and female data (Zar, 1974).

Over the low range of speeds ($0.73\text{--}3.70 \text{ km h}^{-1}$), \dot{V}_{O_2} of female minks increased linearly and was described by the equation:

$$\dot{V}_{O_2} (\text{mlO}_2 \text{g}^{-1} \text{h}^{-1}) = 2.70 + 0.51 \text{ velocity (km h}^{-1}) \\ (r = 0.87, N = 79).$$

The slope of 0.51 was similar to the value of 0.56 predicted for a running mammal of similar body mass (Taylor, Heglund & Maloiy, 1982). However, the oxygen consumption of female minks running at these speeds was consistently higher than predicted. Measured \dot{V}_{O_2} at the point of greatest discrepancy was 2.4 times higher than the predicted level, and occurred at the y-intercept (Fig. 1).

The male mink showed comparable changes in \dot{V}_{O_2} over the same range of speeds. At similar velocities the mass-specific \dot{V}_{O_2} of the male mink averaged 20% lower than that of the females. The relationship between \dot{V}_{O_2} and speed from $0.70\text{--}3.68 \text{ km h}^{-1}$ was:

$$\dot{V}_{O_2} (\text{mlO}_2 \text{g}^{-1} \text{h}^{-1}) = 2.00 + 0.56 \text{ velocity (km h}^{-1}) \\ (r = 0.88, N = 31).$$

At running velocities above 4.13 km h^{-1} the increase in \dot{V}_{O_2} with running speed was described by the linear functions:

$$\dot{V}_{O_2} (\text{mlO}_2 \text{g}^{-1} \text{h}^{-1}) = 2.94 + 0.36 \text{ velocity (km h}^{-1}) \\ (r = 0.84, N = 21)$$

for female minks, and

$$\dot{V}_{O_2} (\text{mlO}_2 \text{g}^{-1} \text{h}^{-1}) = 2.51 + 0.39 \text{ velocity (km h}^{-1}) \\ (r = 0.88, N = 7)$$

for the male mink. Mass-specific \dot{V}_{O_2} of the male mink was approximately 6% lower than the females over the high range of speeds.

Maximum \dot{V}_{O_2}

Maximum \dot{V}_{O_2} determined from plateau levels of the \dot{V}_{O_2} vs work load relationship was:

$$5.90 \pm 0.27 \text{ (s.d.) mlO}_2 \text{g}^{-1} \text{h}^{-1} \text{ (32.80} \pm 1.5 \text{ W kg}^{-1})$$

and

$$6.50 \pm 0.41 \text{ mlO}_2 \text{g}^{-1} \text{h}^{-1} \text{ (36.14} \pm 2.3 \text{ W kg}^{-1})$$

for male and female mink, respectively (Table 1). These levels were approximately nine times basal metabolic rate (BMR) (Farrell & Wood, 1968; Iverson, 1972) and corresponded well with the aerobic scope of ten times BMR for minks (cited in

Table 1. Maximum \dot{V}_{O_2} of the mink

Sex	N	Body weight (g)	$\dot{V}_{O_2, \max}$ (mlO ₂ g ⁻¹ h ⁻¹)	Predicted $\dot{V}_{O_2, \max}$ (mlO ₂ g ⁻¹ h ⁻¹)		
				Taylor <i>et al.</i> (1980)	Pasquis <i>et al.</i> (1970)	Lechner (1978)
Male	1	1019	5.90 ± 0.27	6.96	4.03	3.22
Female	4	868	6.50 ± 0.41	7.18	4.21	3.39

Values for adult minks were determined during inclined running on a treadmill at $T_a = 21^\circ\text{C}$. Measured $\dot{V}_{O_2, \max}$ for minks was within 10–15% of that predicted for a similarly-sized mammal by Taylor *et al.* (1980) for exercise-induced $\dot{V}_{O_2, \max}$ of wild animals. Larger discrepancies are found between maximum values for minks and predicted values derived from cold-exercise-induced $\dot{V}_{O_2, \max}$ (Pasquis, Lacaille & Dejours, 1970; Lechner, 1978).

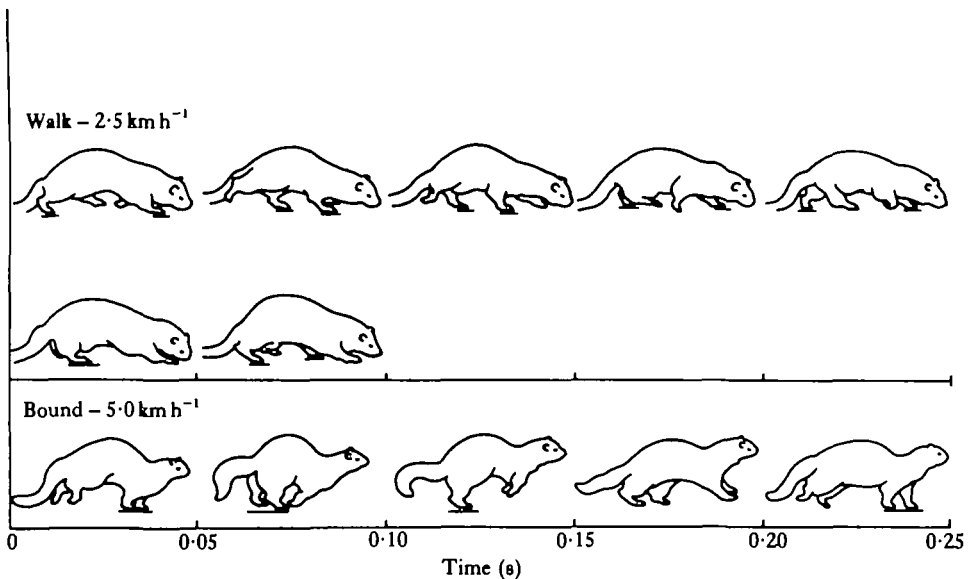


Fig. 2. Walk and half-bound gaits of the mink. One walking stride at 2.5 km h^{-1} took 0.35 s to complete. The bound cycle at 5.0 km h^{-1} was completed in 0.25 s. Note the use of spinal flexion during the bound which is absent when walking.

Morrison, Rosenmann & Estes, 1974) and other mammals (Taylor *et al.* 1980). Values for maximum \dot{V}_{O_2} were more than 22% higher than the greatest level of \dot{V}_{O_2} measured for minks during sustained running. Based on these data it is unlikely that there was a significant anaerobic contribution to metabolism over the range of speeds investigated.

Gait patterns

Over the range of speeds investigated, the minks used two different gaits – walking and bounding (Fig. 2). The walk was observed over the lower range of treadmill speeds. The bound occurred at running speeds greater than 4.0 km h^{-1} , and was characterized by the simultaneous support and propulsion of both hind feet. Since the

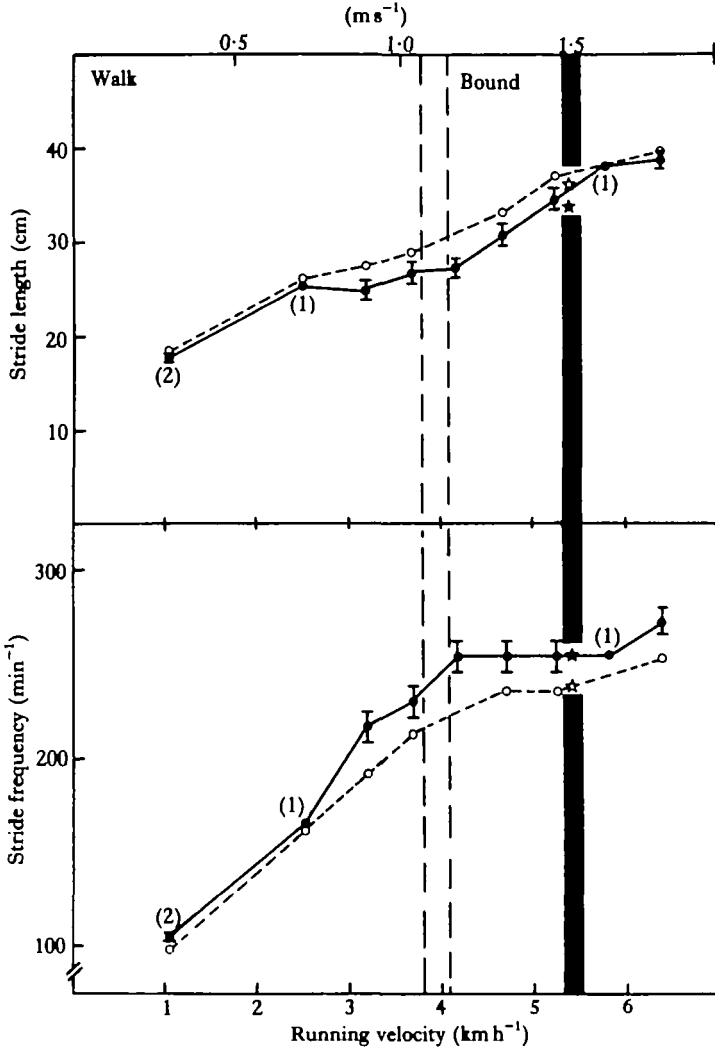


Fig. 3. Stride length and stride frequency plotted as a function of running speed for male (○---○) and female (●—●) minks. Each point denotes a mean value for one male or three females except where otherwise indicated. Thin vertical bars are \pm s.d. The open vertical bar represents the observed transition speeds between gaits for minks. The shaded bar represents the predicted range of speeds for the trot/gallop transition. Stars located within the shaded area are the corresponding stride lengths and stride frequencies for male (★) and female (★) minks predicted at this transition speed for a mammal of similar body mass (Heglund *et al.* 1974).

front feet were not set down in unison, this gait is generally termed the half-bound or the half-paired gallop (Gambaryan, 1974).

The transition between the walk and the half-bound gaits occurred over the range of 3.70–4.17 km h^{-1} for both male and female minks (Fig. 3). The mean gait transition speed for all animals was 3.94 km h^{-1} . In comparison, the predicted trot/gallop transition speed for female minks was 5.32 km h^{-1} (Heglund, Taylor & McMahon, 1974) – 35% higher than the observed speed. The predicted transition speed of 5.52 km h^{-1} for the male mink was 40% higher than measured.

Stride characteristics

Changes in stride frequency and stride length with running speed showed similar trends for both males and females (Fig. 3). Over the walking range of speeds, stride frequency increased with speed, while stride length increased only slightly. During the half-bound, stride frequency remained essentially constant as velocity was increased by increasing the length of the bound. Deviations from these patterns were

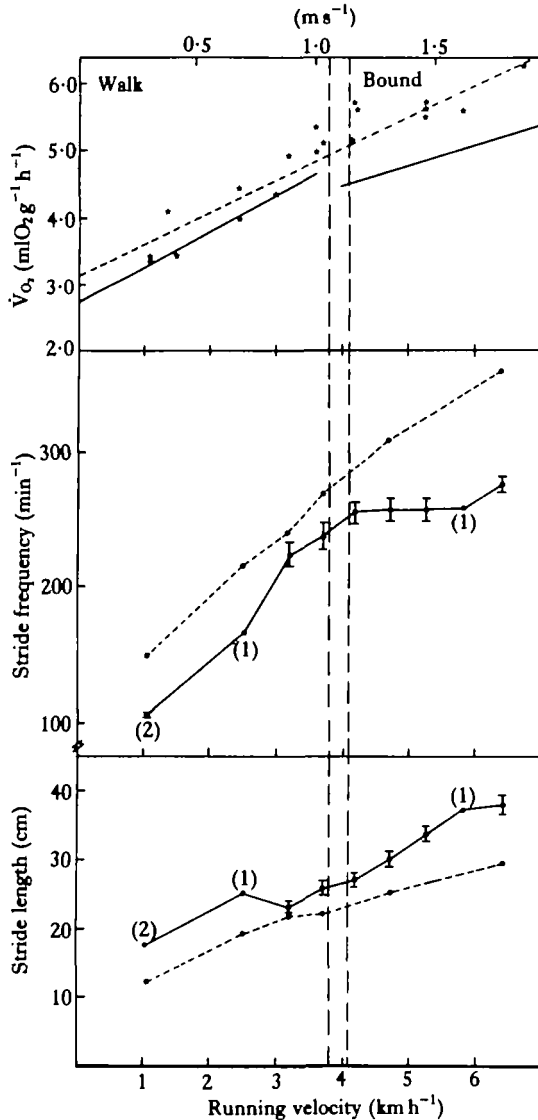


Fig. 4. $\dot{V}O_2$, stride frequency, and stride length in relation to running speed for female minks (solid lines) in comparison to a female mink which did not change gait (dashed lines). The vertical hatched bar represents the normal gait transition speeds. Circles and thin vertical bars are the mean \pm s.d. for three females and the one single-gaited mink except where otherwise indicated. Stars in the upper portion of the graph denote a single experimental bout on the treadmill for the single-gaited mink.

seen at the extremes of the range of speeds. This was due to sporadic movements of the animals at speeds below 1.0 km h^{-1} and an inability to keep up with the tread above 6.50 km h^{-1} . Although the transition between gaits occurred at a lower running velocity than predicted, values for stride frequency at the transition speed coincided well with predictions. Stride length at the transition speed was shorter than predicted; averaging 25 % shorter in females and 21 % shorter in the male.

One of the experimental animals used in this study refused to change gait. Rather than switch to a half-bound at higher speeds, this mink simply continued to increase its walking stride frequency (Fig. 4). The elevated stride frequency, particularly at running speeds above 4.0 km h^{-1} , was associated with a comparatively higher rate of running metabolism for this mink. Over the entire range of speeds, the \dot{V}_{O_2} of this animal increased linearly with running speed and was described by the equation:

$$\dot{V}_{O_2} (\text{mlO}_2 \text{ g}^{-1} \text{ h}^{-1}) = 2.79 + 0.56 \text{ velocity (km h}^{-1})$$

$$(r = 0.94, N = 20).$$

As in the data for walking females, the slope of this relationship, 0.56, is not statistically different from the predicted value of 0.53. Total \dot{V}_{O_2} , however, was more than 40 % higher than expected at all running speeds based on body mass (Taylor *et al.* 1982).

DISCUSSION

Terrestrial locomotion and body morphology

A wide range of locomotor gaits differing in footfall sequence and duration of individual limb movements are employed by terrestrial vertebrates. Despite this variety only two or three different gait patterns are consistently used by each particular species. Individual demands for stability, speed and manoeuvrability, as dictated by body morphology, limit the range of locomotor patterns available to an animal. Consequently, geometrically similar animals tend to select similar gaits which take into account both body shape and mechanical factors associated with movement (Hildebrand, 1980; Alexander, 1977).

Short legs and a long, thin body morphology characteristic of mustelids probably result in locomotor demands that are different from those experienced by more compactly shaped animals. This was reflected in the gait patterns. The two different gaits used by minks during treadmill performances resembled patterns observed for other mustelids (Hildebrand, 1977). Rather than a walk to trot to gallop progression typical of many mammals, minks changed directly from a walk to a half-bound gait with increases in locomotor speed (Fig. 2). Execution of the half-bound by the mink was characterized by spinal flexion which was absent during the walking gait. Likewise, high speed running performance by other mustelids incorporates movements of a flexible, well-muscled spine. When the mustelid bounds, flexion takes place during front limb support and appears to be induced by the inertia of motion rather than active muscular contraction. Forceful extension of the spine occurs during the phase of hind limb support and serves to accelerate the trunk as well as to promote an extended period of flight (Gambaryan, 1974).

This flexibility in conjunction with an elongate body morphology provides both mechanical and energetic advantages during bounding. It was expected that minks, having short legs, would have short stride lengths and high stride frequencies. Instead, observed stride lengths and stride frequencies at the gait transition were similar to those predicted for a mammal of similar body mass but a more conventional body shape (Fig. 3) (Heglund *et al.* 1974). The mink increased its speed above the transition point primarily by increasing the length of the bound. Since changes in stride length originating from limb movements are probably limited in these animals, increases in bound length are undoubtedly aided by spinal mobility.

Movements of the spine during the half-bound probably occur by a combination of active and passive mechanisms in minks. The trunk extends with the simultaneous thrust of both hind paws and flexes upon forepaw impact following an aerial phase. Flexion of the spine during bounding by minks appears to be particularly vulnerable to physical forces associated with motion. By allowing the trunk to 'fold' as the forepaws brake, forward momentum associated with the bound may help to carry the posterior of the animal forward. As a result spinal flexion can take place with a reduced contribution from active muscular contraction and, therefore, at a reduced energetic cost to the animal.

Despite the energetic advantages associated with spinal flexibility, other aspects of the mink's unusual morphology led to elevated locomotor costs (T. M. Williams, in preparation). The oxygen consumption of minks, especially over the range of walking speeds, was higher than predicted for other terrestrial mammals (Fig. 1). The point of greatest discrepancy between predicted and observed running metabolic rates occurred at the y-intercept. Y-intercept values for both male and female minks were more than twice that predicted by Taylor *et al.* (1982). Consequently, transport costs for running minks were comparatively high. The total minimum cost of transport determined from these data was $3.55 \text{ cal g}^{-1} \text{ km}^{-1}$; approximately 25% higher than predicted for similarly sized mammals (Taylor, Schmidt-Nielsen & Raab, 1970).

As observed for minks, the y-intercept for the metabolism *vs* speed relationship of another running mustelid, the ferret, was found by Taylor *et al.* (1982) to be high in comparison to that of other terrestrial mammals. For the ferret, the y-intercept was 56% higher than the predicted value. These elevated metabolic rates for running ferrets and minks prompted the investigation of mustelid metabolism. Many mustelids demonstrate exceptionally high basal metabolic rates (Iverson, 1972; Casey & Casey, 1979), suggesting that the elevated running metabolic rates of both ferrets and minks may be related to high resting rather than high active metabolism. However, unlike other small mustelids which demonstrate high basal metabolic rates, the BMR of minks is only 20% higher than predicted for similarly sized mammals (Iverson, 1972). This slight elevation in BMR contributes little to overall running metabolism in comparison to the metabolic response of minks to activity. Therefore, accounting for the elevated BMR of the mink does not eliminate the large difference between predicted and measured levels of running metabolism. In view of the exceptionally high y-intercept for the \dot{V}_{O_2} *vs* speed function (Fig. 1), perhaps the high energetic cost of running for minks, as well as ferrets, is related to postural effects associated with supporting a long, slender body on short limbs.

Running metabolism and gait

The transition in gait from a walk to a half-bound was coincident with a change in the rate of increase of steady state \dot{V}_{O_2} in minks (Fig. 4). Similar biphasic metabolic responses with running speed have been reported for kangaroos (Dawson & Taylor, 1973) and result in a change in the incremental cost of locomotion (the mass-specific energy expended per distance travelled). Represented by the slopes of the metabolism *vs* speed functions, incremental costs were $0.51 \text{ mlO}_2 \text{ g}^{-1} \text{ km}^{-1}$ for walking, and $0.36 \text{ mlO}_2 \text{ g}^{-1} \text{ km}^{-1}$ for bounding female minks. Comparable differences in cost between the two gaits were also observed for the male mink.

As implied by the decrease in incremental cost at high speeds, the rise in metabolism following transition to the half-bound was less than would have occurred if the walking gait was simply extended over the high range of running speeds. This was supported by the fact that, over the range of speeds when bounding normally occurred, the incremental cost for a mink which refused to change from a walking gait was $0.56 \text{ mlO}_2 \text{ g}^{-1} \text{ km}^{-1}$ (Fig. 4). Thus, changing gaits resulted in a 36% decrease in the incremental cost of transport for these animals. In a study using trained ponies, the extension of gait sequences beyond the natural range of speeds elicited elevated running metabolic rates at the points of gait overlap (Hoyt & Taylor, 1981). These studies suggest that the effectiveness of a gait is limited to a specific range of running speeds in order to be energetically advantageous for the animal.

The energetic savings associated with changing gait may be due to a variety of mechanical or physiological factors. An alternate exchange of potential and kinetic energy, and the storage and recovery of energy from the elastic elements of muscle, act as energy conserving mechanisms during locomotion (Cavagna, Heglund & Taylor, 1977). Since the trunk of the body serves as a potential site for the latter mechanism (Taylor, 1978) and body flexion is a distinct characteristic of high speed locomotion in minks, elastic storage of energy may be important in reducing transport costs during bounding. Alternatively, glycogen depletion studies have shown a selective recruitment of specific muscle fibres coinciding with muscular exertion (Armstrong & Taylor, 1982), limb frequency, and locomotor speed (Armstrong *et al.* 1977). Such a selection process may insure the most efficient employment of the various fibre types.

A frequency-dependent mechanism of energy conservation is especially attractive for minks, as stride frequency plays a major role in determining the metabolic cost of locomotion in these animals (Fig. 5). Regardless of gait, similar frequencies of bounding or walking resulted in similar metabolic rates for minks. The primary influence of locomotor speed and gait upon \dot{V}_{O_2} appears to be the effect these parameters have on stride frequency. While a single bound or step results in similar costs, the distance covered by each are vastly different. A mink using a walking gait at 3.19 km h^{-1} with a stride frequency of $240 \text{ strides min}^{-1}$ incurs approximately the same energetic demand as a bounding animal at 5.26 km h^{-1} with the identical stride frequency. The advantage of the bounding gait resides in the comparatively greater speeds attainable for a given stride frequency. This occurs by virtue of the greater stride lengths afforded by extension of both the trunk and the limbs. Maintenance of the bounding gait at a lower frequency than walking at similar speeds, provides the mink with a mo

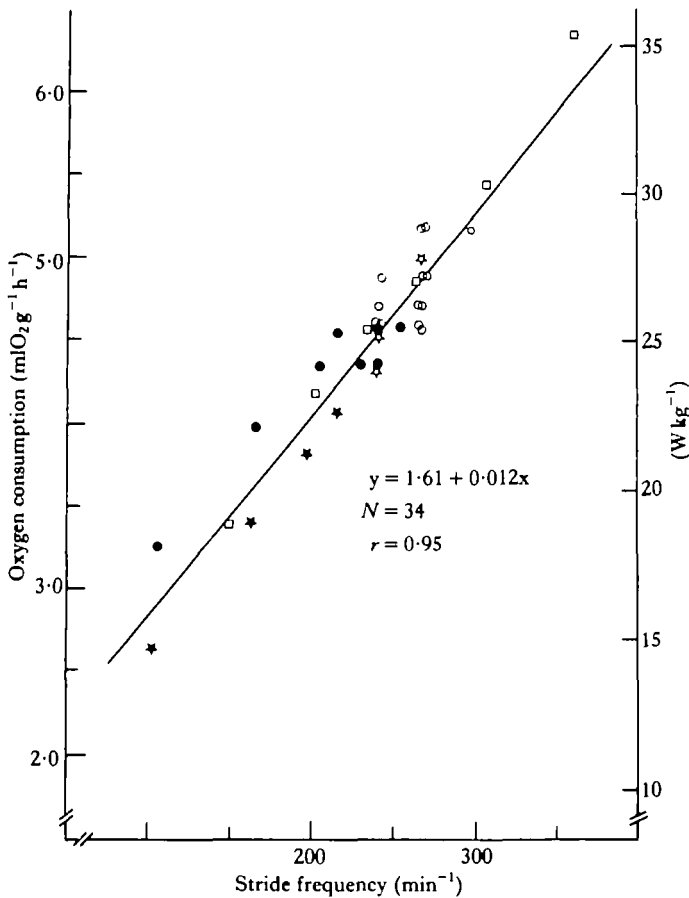


Fig. 5. \dot{V}_{O_2} as function of stride frequency for the mink. ● = walking gait (females), ○ = half-bound (females) and □ = data for the animal which did not change gait. Data for the male mink is represented by ★ (walking), and ☆ (bounding).

efficient means of high speed locomotion. This was optimized by minks through an extension of the bounding range of speeds at the expense of the walking speed range. The transition speed for a mammal of similar body mass to the mink (Heglund *et al.* 1974) averaged 38% higher than observed in this study.

Transition to a half-bounding gait *per se* does not guarantee the same energetic benefits for all animals as observed for minks. Gait patterns like that of the mink are used by a variety of mammals (Hildebrand, 1977; Baudinette, Nagle & Scott, 1976). In contrast to the mink, many of these subjects – including two other mustelids, the ferret (Taylor *et al.* 1982) and the fisher (Powell, 1979) – exhibit linear relationships between \dot{V}_{O_2} and running velocity (Baudinette *et al.* 1976). A comparison of hopping gaits performed by the kangaroo and small hopping bipeds has demonstrated that although similar gait patterns are employed, hopping is a more viable energy conserving strategy for the kangaroo (Thompson, MacMillen, Burke & Taylor, 1980). In both cases, perhaps body size, morphological characteristics, or pressures for high

speed locomotion influence the energetic and mechanical efficiencies associated with these high speed gaits.

In conclusion, the specialized shape of the mustelid has theoretically evolved as a predatory strategy which permits entrance into confined spaces in search of prey (Brown & Lasiewski, 1972). Reduced limb length, and increased body mobility, necessary for navigating rodent burrows, does not appear seriously to limit terrestrial locomotion in the mink. Rather, as suggested by Gambaryan (1974), increased mobility of the spine contributes to the efficiency of the bound, and subsequently compensates for disadvantages associated with short limbs. The selection of specific gait patterns by the mink takes into account the unusual morphology and predatory habits of this animal, and provides both mechanical and energetic advantages.

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