

ENERGETICS OF LOCOMOTION BY THE AUSTRALIAN WATER RAT (*HYDROMYS CHRYSOGASTER*): A COMPARISON OF SWIMMING AND RUNNING IN A SEMI-AQUATIC MAMMAL

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Summary

Semi-aquatic mammals occupy a precarious evolutionary position, having to function in both aquatic and terrestrial environments without specializing in locomotor performance in either environment. To examine possible energetic constraints on semi-aquatic mammals, we compared rates of oxygen consumption for the Australian water rat (*Hydromys chrysogaster*) using different locomotor behaviors: swimming and running. Aquatic locomotion was investigated as animals swam in a water flume at several speeds, whereas water rats were run on a treadmill to measure metabolic effort during terrestrial locomotion. Water rats swam at the surface using alternate pelvic paddling and locomoted on the treadmill using gaits that included walk, trot and half-bound. Water rats were able to run at twice their maximum swimming velocity. Swimming metabolic rate increased with velocity in a pattern similar to the 'humps' and

'hollows' for wave drag experienced by bodies moving at the water surface. Metabolic rate increased linearly during running. Over equivalent velocities, the metabolic rate for running was 13–40% greater than for swimming. The minimum cost of transport for swimming ($2.61 \text{ J N}^{-1} \text{ m}^{-1}$) was equivalent to values for other semi-aquatic mammals. The lowest cost for running ($2.08 \text{ J N}^{-1} \text{ m}^{-1}$) was 20% lower than for swimming. When compared with specialists at the extremes of the terrestrial–aquatic continuum, the energetic costs of locomoting either in water or on land were high for the semi-aquatic *Hydromys chrysogaster*. However, the relative costs for *H. chrysogaster* were lower than when an aquatic specialist attempts to move on land or a terrestrial specialist attempts to swim.

Key words: water rat, *Hydromys chrysogaster*, swimming, running, wave drag, locomotion, energetics.

Introduction

Semi-aquatic mammals best represent the transitional forms that gave rise to highly derived aquatic mammals. However, these animals occupy a precarious evolutionary position by having to function in both aquatic and terrestrial environments without specializing in their locomotor performance in either environment. Semi-aquatic mammals have been restricted to morphologies and swimming behaviors that are energetically expensive (Fish, 1992, 1993a; Williams, 1998). The various body forms show little streamlining and the propulsive appendages, although larger than in their terrestrial counterparts, are relatively smaller than in fully aquatic mammals (Howell, 1930; Mordvinov, 1976; Stein, 1981; Williams, 1989; Fish, 1993a; Thewissen and Fish, 1997). The use of paddling by many semi-aquatic mammals, as a mechanism for aquatic propulsion, incurs a low mechanical efficiency because of limited thrust production, increased drag during the recovery phase of the stroke cycle and high energy losses from inertial and added mass effects (Fish, 1984, 1992). In addition, semi-aquatic mammals generally swim at the air–water interface, where energy losses are high as a result of

the addition of wave drag (Hertel, 1966; Fish, 1982; Williams, 1983a, 1989).

Whereas swimming by semi-aquatic mammals is associated with inefficiencies and high energetic costs, the converse is considered true for terrestrial locomotion. Williams (1983a,b) found that mink (*Mustela vison*) had a greater mass-specific metabolic rate when swimming than when running at equivalent speeds. However, mink display a quadrupedal mode of swimming and few adaptations to enhance swimming performance (Williams, 1983a, 1989; Fish, 1993a), which is indicative of more terrestrial species.

Unfortunately, there is a paucity of direct comparisons of locomotor energetics between running and swimming for semi-aquatic species. Besides mink, the only other mammals for which comparative data for running and swimming are available are humans (Holmér and Åstrand, 1972; DiPrampo, 1986). Although humans display the same maximum rate of oxygen consumption for both types of locomotion, they do so at a running speed at least twice as fast as they can swim (Holmér and Åstrand, 1972).

Fish (1992) suggested that investigations of locomotor energetics by semi-aquatic species should employ an experimental design involving direct comparisons of terrestrial and aquatic performance. Examinations of this type would provide insight into the compromises inherent in the physiological and morphological adaptations that operate in two physical environments. These studies of intermediate animals would indicate which potential selective factors and mechanical constraints may have directed the evolution of the more derived aquatic species.

The purpose of this study was to compare the energetics of swimming and running in a semi-aquatic mammal, the Australian water rat (*Hydromys chrysogaster* Geoffroy). The water rat is an amphibious murid rodent restricted to Australia, New Guinea and some adjacent islands (Strahan, 1995). The water rat dives and forages under water (Woollard et al., 1978). It feeds on some plant material and is essentially an opportunistic predator of crustaceans, hard-shelled molluscs, fish, frogs, lizards, water birds and carrion (Troughton, 1941; Barrow, 1964; Strahan, 1995). Its aquatic adaptations include a dense, waterproof pelage and partially webbed hindfeet (Howell, 1930; Troughton, 1941; Dawson and Fanning, 1981; Strahan, 1995). Metabolic rates of water rats swimming in a flume and running on a treadmill were compared over a wide range of speeds. This comparison demonstrated energetic compromises associated with locomotion in vastly different environments.

Materials and methods

Animals

Six adult water rats *Hydromys chrysogaster* Geoffroy (three of each sex) used in this study were trapped in the Torrens River near Adelaide, South Australia, and at Lake Alexandrina near Murray Bridge, South Australia. The animals were caught in cage traps under State Department of Environment permits. The animals were released at the site of capture after the experiments. The range of body masses was 470.5–959.4 g (721.4 ± 133.4 g; mean \pm S.D.). In the laboratory, the animals were housed singly in outdoor covered pens and maintained on a diet of small fish and crustaceans. Nesting boxes and a small swimming pond were provided.

Swimming flume

Swimming experiments were conducted in a recirculating flume based on a design of Vogel (1981). Water was circulated around the vertical annulus using a variable-speed electric motor driving a propeller. A working section was defined by parallel acrylic baffles 27.5 cm apart, and the upstream and downstream ends of the section were formed from mesh to confine the animals. Turbulence in the working section of the water channel was reduced with a flow screen formed from an array of fine tubes, the internal diameter to length ratio being 1:10. Profiles of water flow within the test section were measured using a calibrated flow meter (Global Water), and turbulence was assessed from video tapes of the loci of fine

particulate matter introduced into the water current. The results indicated that flow rates did not vary in regions in which the animals swam and that turbulence was undetectable.

The top of the working section consisted of a metabolic chamber with a slanted roof of dimensions 26 cm \times 26 cm \times 7 cm formed by a clear acrylic plastic cover bounded by flexible side panels. The acrylic plastic extended upstream and downstream of the base of the chamber as broad aprons that covered the remainder of the working section and formed a seal under the water surface. Visual inspection demonstrated that the aprons produced no turbulence in the working section. The metabolic chamber had inlet and outlet ports for the introduction and removal of air, respectively. Mean water temperature was maintained at 24.8 ± 0.3 °C.

The animals were trained to swim in the apparatus over a period of 2 weeks. Trials were randomised over a speed range of 0.33–0.68 m s⁻¹. Each trial lasted for between 6 min for the higher speeds and 12 min at slow swimming speeds.

Metabolic and kinematic measurements

Measurements of oxygen consumption were taken from the fractional oxygen and carbon dioxide concentrations of air drawn through the chamber at flow rates of 12 l min⁻¹ using a pump (40 W Reciprotor AB, type 506). The flow was regulated by a mass-flow controller (Sierra Instruments, model 840 NT) previously calibrated against a Brooks volumeter. A 100 ml min⁻¹ subsample of gas was drawn from the air flow exiting the chamber using an Ametek R-1 flow control (Applied Electrochemistry). The subsample was dried by passing it through a column of Drierite (CaSO₄). The fractional concentrations of O₂ and CO₂ were determined from the subsample using an Ametek carbon dioxide analyser (CD-3A) with a P61B sensor and Ametek oxygen analyser (S-3A/I) with a N-22M sensor, respectively. The output from the instruments was digitised using a universal interface (Sable Systems) to a Toshiba T3100SX portable microcomputer. Metabolic analyses were performed using the Sable Systems DATACAN V software package. The metabolic determinations are based on equation 4b of Withers (1977). Any drift in the monitoring system was corrected by linear interpolation between initial and end baseline readings taken with the flume running. The volume and flow characteristics of the chamber were such that the time required to reach 99% of equilibrium was 42 s. This was much less than the swim times of between 6 and 12 min. Data reported are from steady-state measurements with less than 5% variation over a 3 min period. The energetic equivalent of the rate of O₂ consumed at STPD, representing metabolic rate, was calculated using the standard conversion factor of 20.1 J ml⁻¹ O₂ for an animal that was not post-absorptive.

The resting rates of oxygen consumption of animals could not be measured because of their level of activity in the flume. When placed in the flume, animals swam continually and dived as they probed the working section.

Video-taped recordings were made during swimming trials for the determination of swimming gaits and stroke lengths.

Swimming motions were recorded using a JVC video camera (model TK 128 IEG). The camera was positioned to record images parallel to the water surface and from beneath the animal *via* a mirror placed at 45° to the transparent base of the working section. Sequential frames of video tape (1/50 s) were viewed using a Blaupunkt RTV-966 video recorder. Data were collected on stroke frequency.

Treadmill

Measurements of rates of oxygen consumption during terrestrial locomotion were taken from five of the animals as they moved on a motor-driven treadmill. The treadmill had a belt runway that was 1 m in length and 0.4 m wide. The animals adapted readily to this regime and learned to maintain their position on the treadmill after 1–2 days of training. Speeds varied between individual animals, but for the group as a whole a range between 0.25 and 1.77 m s⁻¹ was achieved, although measurements of oxygen consumption were only possible for animals running at speeds no greater than 1.42 m s⁻¹. Mean air temperature was 23.9±1.2 °C.

Rates of oxygen consumption were determined from fractional concentrations of O₂ and CO₂ in air drawn from a light mask made from acetate sheeting attached to the animal's head with a collar. With the exception of one individual that had to be removed from the sample, the animals readily accepted the mask and could maintain steady-state metabolic levels over the 3–4 min of the experimental period. The time required to reach 99% of equilibrium using the mask was 7 s.

Air was drawn through the masks at regulated flows of 7 l min⁻¹. To test for leaks of exhalant gas around the animal's head, the flow was increased by 50% for some duplicate runs, a procedure that resulted in the same calculated metabolic levels. Metering of nitrogen gas into the mask also indicated no leakage from the system. A subsample of the gas was pumped to the same gas analysis system as described above for the swimming experiments.

Gait analysis and step frequency were determined from video-taped records, using the equipment described above, taken parallel to the treadmill surface. Gaits were determined using methods developed by Hildebrand (1980). Frequency was determined from the inverse of the period of a complete cycle of motion, averaged over five cycles.

All regressions and correlation coefficients, *r*, were calculated using KaleidaGraph software (version 3.0.2). Correlation coefficients were determined to be statistically significant at a level of *P*<0.05.

Results

Locomotor movements

In the water flume, water rats displayed positive buoyancy and were able to swim with their nostrils and dorsum of the head and body above the water surface (Fig. 1). The longitudinal axis of the body was roughly parallel to the water surface or canted at a slight angle, and the spine was extended. The forelimbs were held out anteriorly, held ventrally or tucked under the chin. Motions by neither the tail nor the forefeet appeared to provide

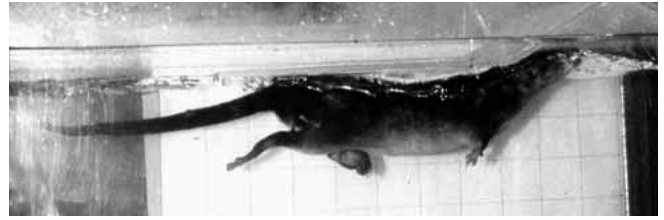


Fig. 1. Swimming strokes of water rat *Hydromys chrysogaster*. The animal is swimming with nostrils, eyes and dorsum above the water surface. The hindfeet show an alternate paddling stroke, with one foot in the power phase and the other foot in the recovery phase. A bow and stern wave were evident, with the body contained within the wave trough.

propulsion. Short pawing motions of the forelimbs were sometimes observed when the rats were adjusting their position.

Propulsion was accomplished by alternate paddling motions of the hindfeet in the parasagittal plane (Figs 1, 2). The paddling cycle consisted of power and recovery phases. These movements were qualitatively similar to alternate hindfoot paddling described by Fish (1984) for muskrat (*Ondatra zibethicus*). During the power phase (Fig. 1), the hindfoot was swept posteriorly with the digits extended and abducted (spread). During recovery (Fig. 1), the hindfoot was swept anteriorly with the digits plantarflexed and adducted (pulled together).

Three quadrupedal gaits were used by the water rats during terrestrial locomotion, including the walk, trot and half-bound (Hildebrand, 1980). Walks and trots were characterized as symmetrical gaits in which the limbs alternated so that three feet were in contact with the ground simultaneously and two diagonal feet simultaneously contacted the ground, respectively (Fig. 2). The half-bound represented an asymmetrical gait in which the hindfeet provided simultaneous support and propulsion and the forefeet were not set down in unison (Williams, 1983b). Choice of gaits was dependent on speed, with walks used at speeds less than 0.62 m s⁻¹, trotting at 0.62–1.30 m s⁻¹ and half-bounds at speeds greater than 1.3 m s⁻¹.

Frequency (*f*) of the swimming stroke cycle was independent of velocity (*U*) (Fig. 3). Mean *f* was 1.28±0.11 Hz (mean ± s.d., *N*=41). In contrast, the frequency of the step cycle for terrestrial locomotion showed a significant (*P*<0.001; *r*=0.95; d.f.=31) linear increase with increasing *U* (Fig. 3). The equation describing the relationship is:

$$F = 1.77 + 1.97U, \quad (1)$$

where *f* is in units of Hz and *U* is in m s⁻¹.

Locomotor metabolism

When swimming at the water surface, the mass-specific metabolic rate (\dot{V}_{O_2}) was dependent on *U* (Fig. 4). \dot{V}_{O_2} increased curvilinearly with *U* and was best described by a third-order polynomial equation:

$$\dot{V}_{O_2} = -5.96 + 50.95U - 107.60U^2 + 77.78U^3, \quad (2)$$

where \dot{V}_{O_2} is in units of ml O₂ g⁻¹ h⁻¹. The equation was highly significant (*P*<0.001; d.f.=39), with *r*=0.86. Over the range of

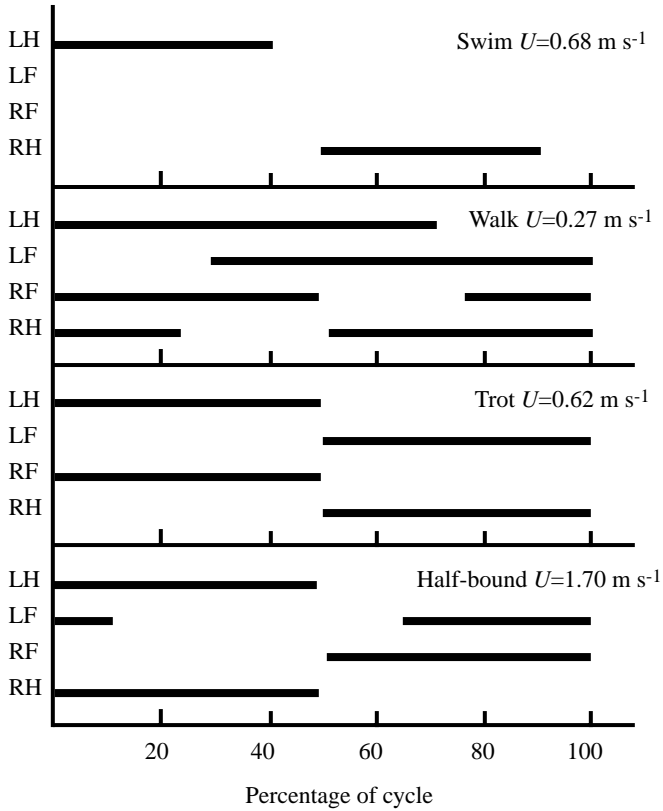


Fig. 2. Gait diagrams for aquatic and terrestrial locomotion by *Hydromys chrysogaster*. Horizontal bars indicate the time as a percentage of the power phase cycle during swimming, and time as a percentage of the cycle that the feet contact the ground for the walk, trot and half-bound. The abbreviations along the vertical axis indicate the left hindfoot (LH), left forefoot (LF), right forefoot (RF) and right hindfoot (RH). Swim cycle time was 0.81 s, and cycle times for terrestrial locomotion at 0.27, 0.62 and 1.70 m s⁻¹ were 0.49, 0.33 and 0.20 s, respectively. U , velocity.

U (0.33–0.68 m s⁻¹), mean \dot{V}_{O_2} increased by 76%. Similar polynomial functions have been used to describe the relationship between metabolic rate and speed for submerged swimming by pygoscelid penguins (Culik et al., 1994), beaver (Allers and Culik, 1997) and otters (Pfeiffer and Culik, 1998).

The mass-specific metabolic rate increased linearly with speed during terrestrial locomotion (Fig. 4). The equation describing the relationship is:

$$\dot{V}_{O_2} = 2.51 + 2.07U, \quad (3)$$

which was significant ($P < 0.001$; d.f.=16; $r=0.92$). Over an 11-fold increase in velocity (0.13–1.42 m s⁻¹), \dot{V}_{O_2} increased by 96%.

Over an equivalent range of velocities, the \dot{V}_{O_2} for terrestrial locomotion was greater than the \dot{V}_{O_2} for swimming (Fig. 4). At low velocities (<0.40 m s⁻¹), swimming \dot{V}_{O_2} was 35–40% lower than running \dot{V}_{O_2} , whereas swimming \dot{V}_{O_2} was only 13% lower than running \dot{V}_{O_2} at 0.68 m s⁻¹. In addition, \dot{V}_{O_2} at the maximum running velocity was 1.6 times greater than the maximum \dot{V}_{O_2} attained during swimming.

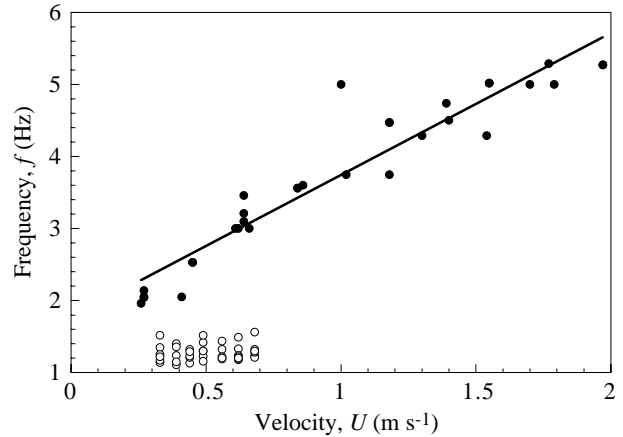


Fig. 3. Frequency (f) versus velocity (U). Filled circles are for terrestrial locomotion, and open circles are for swimming. The equation for the regression line for terrestrial locomotion is provided in the text.

In comparison with data collected previously on *H. chrysogaster*, the maximum metabolic rate observed in this study was 1.6 times the peak value measured by Dawson and Fanning (1981).

Cost of transport

Cost of transport (COT) was used to compare directly the efficiency of aquatic and terrestrial locomotor energetics from the measurements of metabolic effort (Tucker, 1970, 1975; Schmidt-Nielsen, 1972; Videler and Nolet, 1990; Videler, 1993). COT is the metabolic cost of moving a unit mass over a given distance and is inversely proportional to efficiency (Tucker, 1970). COT was calculated as:

$$\text{COT} = \text{MR}(M \times g \times U)^{-1}, \quad (4)$$

where MR is the metabolic rate in J s⁻¹, M is body mass in kg,

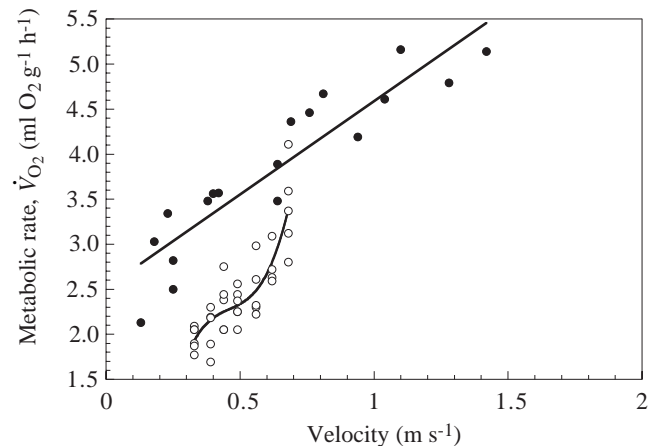


Fig. 4. Metabolic rate, indicated by mass-specific rate of oxygen consumption (\dot{V}_{O_2}), as a function of velocity (U). Filled circles are for terrestrial locomotion, and open circles are for swimming. The relationship between metabolic rate and velocity is best described as a straight line for terrestrial locomotion and as a third-order polynomial for swimming. Equations for these lines are provided in the text.

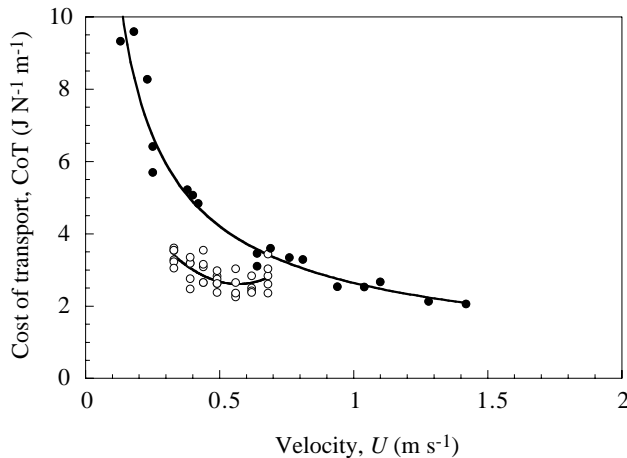


Fig. 5. Cost of transport (COT) as a function of velocity (U). Filled circles are for terrestrial locomotion, and open circles are for swimming. The relationships between COT and U are described as a power function for terrestrial locomotion and as a second-order polynomial for swimming. Equations for these lines are provided in the text.

g is the gravitational acceleration (9.8 m s^{-2}), and U is velocity in m s^{-1} (Videler and Nolet, 1990). The units of COT are $\text{J N}^{-1} \text{m}^{-1}$, which makes COT dimensionless.

COT for swimming varied parabolically with U (Fig. 5) and was described by the equation:

$$\text{COT} = 7.11 - 15.84U + 13.92U^2. \quad (5)$$

This equation was highly significant ($P < 0.001$; d.f.=39; $r = 0.68$). The minimum COT and its corresponding U were calculated from the minimum of the first derivative of equation 5. Minimum COT was $2.61 \text{ J N}^{-1} \text{m}^{-1}$ and occurred at $U = 0.57 \text{ m s}^{-1}$.

COT for terrestrial locomotion decreased curvilinearly with increasing U towards an asymptote according to the equation:

$$\text{COT} = 2.64U^{-0.67}. \quad (6)$$

The data were significantly correlated ($P < 0.001$; d.f.=16; $r = 0.97$). Although no minimum value of COT was reached, the lowest value of COT was $2.08 \text{ J N}^{-1} \text{m}^{-1}$ at $U = 1.42 \text{ m s}^{-1}$. This COT value for running was 20% lower than the minimum COT for swimming.

Discussion

Swimming mode and terrestrial gaits

Fish (1996) argued that the various swimming modes utilized by mammalian swimmers were derived from terrestrial gaits which were modified from conservative motor patterns. Paddling by alternating movements of the limbs represents a modification of a symmetrical gait such as a walk or trot (Fish, 1993a, 1996). Furthermore, the shift from a quadrupedal paddling mode to alternating bipedal paddling was accomplished by the control of buoyancy through the acquisition of nonwetable fur.

H. chrysogaster could use alternate pelvic paddling effectively because of its ability to gain buoyancy and to maintain trim from air entrapped in its dense fur. Hair density for *H. chrysogaster* has been estimated to be $169\text{--}363 \text{ hairs mm}^{-2}$ (Dawson and Fanning, 1981) and $410\text{--}488 \text{ hairs mm}^{-2}$ (F. E. Fish and R. V. Baudinette, unpublished data). Although the hair density for *H. chrysogaster* is lower than that of the platypus (*Ornithorhynchus anatinus*) ($837 \text{ hairs mm}^{-2}$; Grant and Dawson, 1978), which shares the same habitats, it is within the range ($350\text{--}507 \text{ hairs mm}^{-2}$) of the river otter *Lutra lutra* (Sokolov, 1982).

The alternate pelvic paddling mode used by *H. chrysogaster* displayed the same gross movements typical of other semi-aquatic mammals (Howell, 1930; Tarasoff et al., 1972; Fish, 1984, 1993b, 1996). The paddling mode is inherently inefficient because thrust is generated only through approximately half of the stroke cycle and increased drag is incurred during the recovery phase of the cycle. Mechanical efficiencies for paddling rodents were calculated at 25–33%, whereas swimming modes based on lifting hydrofoils (i.e. dolphin flukes, sea lion flippers) have efficiencies of over 70% (Fish, 1984, 1992, 1996; Feldkamp, 1987; Liu and Bose, 1993).

Despite its semi-aquatic habits, the pattern of limb movement on land by *H. chrysogaster* appeared to be similar to gaits and kinematics displayed by terrestrial rodents (Hildebrand, 1976). At low speeds the symmetrical walk is employed, and at moderate speeds the trot is employed. Gallops, bounds and half-bounds are used at rapid speeds. The use of defined gaits within an optimal range of speeds and frequencies corresponds to a reduction in peak stresses and energy costs (Hoyt and Taylor, 1981; Farley and Taylor, 1991). Heglund and Taylor (1988) found that the frequency of limb movement associated with a gait transition could be predicted from body mass. For *H. chrysogaster*, the predicted frequency at the minimum trotting speed was 2.49 Hz, which is 17% lower than the frequency derived from equation 1. However, the predicted frequencies for the preferred trotting speed (3.50 Hz) fell within the range of observed trotting frequencies (2.99–4.33 Hz), and the predicted frequency for the trot–gallop transition was less than 2% higher than the observed value.

The relationship between the frequency of the propulsive cycle and U for *H. chrysogaster* was different for swimming and terrestrial locomotion. However, these patterns were similar to those displayed by aquatic and terrestrial animals. Paddling animals typically use a single propulsive frequency that does not vary with swimming speed. Constant frequencies have been reported for ducks (Prange and Schmidt-Nielsen, 1970; Aigeldinger and Fish, 1995), human competition swimmers (Nadel, 1977), mink (Williams, 1983a), muskrats (Fish, 1984) and sea otters (Williams, 1989). For terrestrial locomotion, stride frequency increases with U in a linear fashion, where the slope of the line is determined by the body mass (Heglund et al., 1974; Heglund and Taylor, 1988). However, at high running speeds, the stride frequency becomes

independent of U . This shift in frequency is believed to correspond to the use of elastic storage of energy in the musculoskeletal system, which reduces the energy cost of locomotion (Heglund et al., 1974; Heglund and Taylor, 1988). Above the transition from trot to gallop, the effect is increased because of the incorporation of elastic elements in both the legs and trunk (Heglund et al., 1974; Alexander, 1988, 1991). The use of elastic storage in the musculoskeletal system of swimming vertebrates has also been hypothesized as a mechanism for energy economy (Bennett et al., 1987; Blickhan and Cheng, 1994; Clark and Fish, 1994; Pabst, 1996; Long et al., 1997), although no direct evidence exists for a springlike system.

The use of elastic storage mechanisms, however, seems doubtful for running or swimming by *H. chrysogaster*. Unlike large quadrupeds, the stride frequency of *H. chrysogaster* when galloping continued along the same linear slope displayed at lower speeds. A constant frequency above the trot–gallop transition would have indicated that the animal was using a tuned spring system (Taylor, 1985). By oscillating the body and limbs at a constant frequency, specific muscles and tendons that resonate at the same frequency can be used to move the animal economically (Taylor, 1978). Although frequency remains constant during swimming, the paddling mode used by *H. chrysogaster* does not adhere to a resonant model (Clark and Fish, 1994). Indeed, the compromise between the requirements for swimming and walking may prohibit the musculoskeletal system from forming resonant systems. Finally, the cost of locomoting on land or in water is high compared with more specialized animals (see below) negating possible energy-saving mechanisms.

Aquatic and terrestrial energetic performance

Our results demonstrate distinct differences in the energetic performance of a semi-aquatic mammal operating in either aquatic or terrestrial environments. In *H. chrysogaster*, the metabolic rate increased curvilinearly with speed when swimming, whereas a linear trend was observed for running. The patterns of metabolic increase with U reflected differences in the forces encountered in moving through water or on land.

When swimming, the active metabolic rate, representing the power input, is used to generate thrust and overcome the hydrodynamic resistance (drag), which increases curvilinearly (Webb, 1975; Vogel, 1981). Previous studies of swimming mammals showed this trend for metabolic rate (Holmér, 1972; Davis et al., 1985; Feldkamp, 1987; Williams, 1983a; Allers and Culik, 1997). It is typically assumed that the metabolic rate will increase as a power function (i.e. $y=ax^b$) with an exponent (b) greater than 1 (Videler, 1993), because the drag power, representing the power output, increases with the cube of the velocity (Webb, 1975; Vogel, 1981; Fish, 1992). However, a simple power function relationship was not observed for *H. chrysogaster*, for which the active metabolic rate was described with a polynomial function with respect to U .

The difference between theory (power function) and observation (polynomial) can be explained by the components

of drag and the position of the body with respect to the water surface. Expectation of a power function relationship assumes that the drag experienced is for a fully submerged body. The drag for a submerged body has frictional (viscous) and pressure (form) components (Webb, 1975; Vogel, 1981). The frictional component dominates for submerged, streamlined bodies. However, for bodies moving at or near the water surface, a wave drag component is added to the total drag (Marchaj, 1964; Hertel, 1966; Fish, 1993a). The wave drag becomes the dominant component of drag, with a magnitude of up to five times the frictional drag (Hertel, 1966). Wave drag results from the conversion of kinetic energy from a body's motion into potential energy in the formation of waves (Marchaj, 1964; Fish, 1993a; Videler, 1993). The increased drag from wave formation requires greater energy expenditures for animals swimming at the surface compared with submerged swimming (Lang and Daybell, 1963; Prange and Schmidt-Nielsen, 1970; Fish, 1982, 1992, 1993a; Williams, 1983, 1989; Baudinette and Gill, 1985; Webb et al., 1991; Videler, 1993).

While moving at the water surface, a body will produce two distinct series of waves, which are referred to as the bow-wave system and the stern-wave system (Taylor, 1933). These systems are composed of diverging and transverse waves which each contribute half of the wave drag (Hoerner, 1965). The diverging waves from the bow and stern cannot interfere with one another; however, the transverse bow waves can be superimposed on the transverse stern waves because wavelength is variable and dependent on the speed of the body (Marchaj, 1964; Hoerner, 1965). With increasing speed, the wavelength of the bow-wave system increases and the bow waves interact with the waves generated at the stern. Depending on the phase relationship, the bow and stern waves can produce a positive or negative interference. Thus, the drag on a body can be exaggerated when wave crests are synchronized and can be reduced when a wave crest and trough interfere destructively. As a result, for a body moving at the surface, the drag as a function of velocity shows 'humps' and 'hollows' (Fig. 6; Taylor, 1933; Hoerner, 1965).

The pattern of humps and hollows is dependent on the relationship between the waterline length of the body (L_w) and the velocity (U), expressed as the dimensionless Froude number (F_L):

$$F_L = U/\sqrt{gL_w}, \quad (7)$$

where g is the gravitational acceleration (9.8 m s^{-2}). Humps occur at critical F_L values of 0.20, 0.28 and 0.45, with hollows between these values (Taylor, 1933; Hoerner, 1965). As measured from video recordings, L_w for *H. chrysogaster* was $0.27 \pm 0.03 \text{ m}$ (mean \pm s.d., $N=37$) so that *H. chrysogaster* swam over a range of F_L of 0.20–0.42.

For surface-swimming *H. chrysogaster*, the increase in \dot{V}_{O_2} with U indicates a complex pattern reminiscent of the humps and hollows for bodies at the surface rather than the simple power function of submerged bodies (Figs 4, 6). Comparison between trends in mean \dot{V}_{O_2} for *H. chrysogaster* and wave drag for a model ship hull in a towing tank demonstrate similar

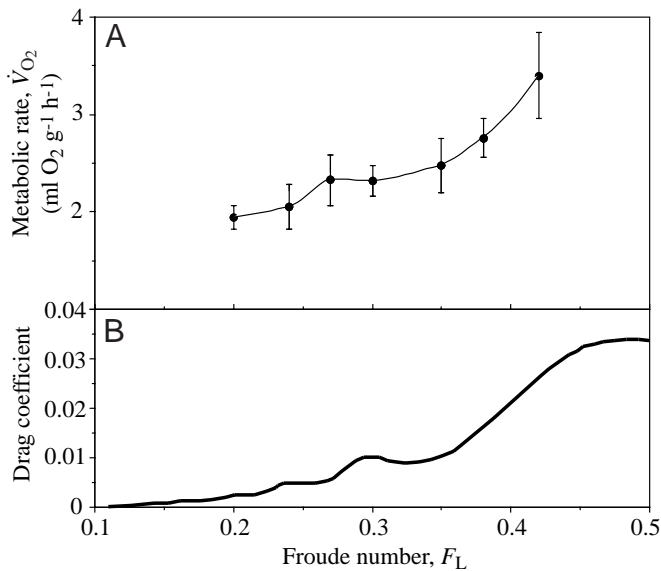


Fig. 6. Comparison of trends of mean metabolic rate (\dot{V}_{O_2}) (\pm s.d.) of surface-swimming *Hydromys chrysogaster* (A) with wave drag for a model ship hull (B; redrawn from Hoerner, 1965) with respect to Froude number. Froude number (F_L) was calculated as $F_L = U/\sqrt{gL_w}$, where U is the velocity (in m s^{-1}), g is the gravitational acceleration (9.8 m s^{-2}) and L_w is the waterline length (in m).

humps at the critical F_L of 0.28 (Fig. 6). This suggests that the energetics of surface swimming by *H. chrysogaster* is sensitive to changes in wave drag and that the use of a polynomial to fit the data is appropriate.

For terrestrial locomotion, the metabolic rate is affected by ground reaction forces associated with oscillations of the body mass (Taylor, 1985; Full, 1989). Energy is consumed, with fluctuations of kinetic and gravitational potential energy due to changes in horizontal and vertical forces. The oscillations are correlated with the pattern of footfalls expressed as defined gaits. The ability of terrestrial animals to change gait is responsible for the linear increase of \dot{V}_{O_2} with speed. Switching gaits allows an animal to minimize its metabolic energy cost over a range of speeds while reducing bone and muscle stresses (Hoyt and Taylor, 1985; Taylor, 1985; Farley and Taylor, 1991).

The influence of conflicting forces requires morphological and physiological trade-offs for mammals that operate in both terrestrial and aquatic regimes. The expected consequence of these trade-offs would be variable energetic effectiveness associated with the degree of adaptation to either environment. Over an equivalent range of speed, the semi-aquatic *H. chrysogaster* exhibited a lower metabolic rate during swimming compared with terrestrial locomotion. The lower metabolic rate for swimming could reflect morphological adaptations associated with increased aquatic habits. The change from quadrupedal terrestrial locomotion to bipedal paddling would accompany a decrease in metabolic effort as a result of the reduction in muscle mass in active use.

Despite their aquatic habits, mink (*Mustela vison*) are not considered to have an obligatory association with water (Estes,

1989). Indeed, their morphology and behavior suggests a more terrestrial polarity. Mink use a modified terrestrial, quadrupedal gait to swim (Williams, 1983a) and have bone densities that are similar to those of terrestrial mustelids (Fish and Stein, 1991). In addition, the propulsive surface area of the mink's paws is only 1% of the total surface area compared with over 5% for the related aquatic sea otter (*Enhydra lutris*) (Williams, 1989). The maximum mass-specific metabolic rate for swimming mink was 1.6 times that for running at equivalent speeds of 0.7 m s^{-1} . Running mink attained their maximum metabolic rate at a speed nearly 1.0 m s^{-1} faster than swimming. At the opposite pole of the terrestrial-aquatic continuum, the sea lion (*Zalophus californianus*) had a metabolic cost for swimming that was lower than that of comparatively sized mammalian runners at the same speeds (Feldkamp, 1987).

These data suggest a reversal of metabolic effectiveness along the terrestrial-aquatic continuum, but comparisons of metabolic rates over similar velocities may not be equivalent because of the differences in the densities of the media and the predominant external forces that limit performance. Although a maximum \dot{V}_{O_2} of $5.45 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ for running *H. chrysogaster* was attained at 1.42 m s^{-1} , this value was not reached by *H. chrysogaster* when swimming (Fig. 4).

The higher swimming speeds necessary to reach the same maximum value of \dot{V}_{O_2} may not have been attainable because of a physical limitation to the maximum speed when moving at the water surface. This speed is referred to as 'hull speed' (Prange and Schmidt-Nielsen, 1970). Hull speed is due to the constructive interference between transverse waves created at the bow and stern of a body or hull. With increasing speed, the wavelength of these waves increases until the wavelength of the bow wave matches the hull length of the body, so that the second crest of the bow wave is superimposed upon the first crest of the stern wave (Taylor, 1933; Marchaj, 1964). At that time, the animal becomes trapped in a wave trough of its own creation, and further increases in speed would only be possible by expending large amounts of energy to swim through or over the bow wave (Prange and Schmidt-Nielsen, 1970; Fish, 1996). Surface-swimming animals rarely exceed the hull speed and do so only by using extraordinary behaviors (Aigeldinger and Fish, 1995).

The hull speed (U_h) is directly dependent on L_w according to:

$$U_h = \sqrt{(L_w g / 2\pi)}. \quad (8)$$

U_h for *H. chrysogaster* was estimated to be 0.64 m s^{-1} . This speed was close to the maximum speed attained in this study, indicating a restriction to further increases in velocity with increased metabolic effort. Similar restrictions have been noted for a variety of surface-swimming birds and mammals (Prange and Schmidt-Nielsen, 1970; Fish, 1982; Williams, 1983a; Baudinette and Gill, 1985; Aigeldinger and Fish, 1995). U_h is typically associated with a smaller increase in \dot{V}_{O_2} compared with the metabolic increase at maximum locomotor speeds of terrestrial endotherms (Baudinette and Gill, 1985).

Cost of transport

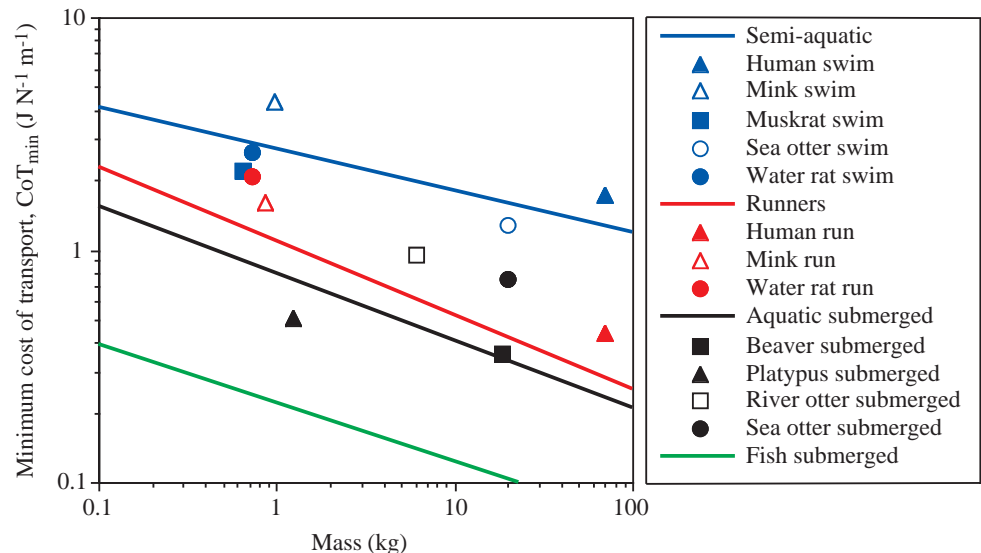
Examination of the minimum cost of transport (COT_{min}) represents an approach whereby locomotor energetics can be compared without consideration of velocity (Videler, 1993). Typically, the minimum costs for various locomotor modes (e.g. swimming, flying, running) are different (Tucker, 1970, 1975). Despite movement through a denser medium, swimming animals, exemplified by fish, have the lowest COT_{min} for their body size, whereas terrestrial animals have the highest. The rationale for this relationship is that swimmers are nearly neutrally buoyant and do not have to expend additional energy to support their bodies against gravity as do terrestrial animals (Schmidt-Nielsen, 1972; Videler and Nolet, 1990). However, the relationship between runners and swimmers is reversed when the swimmers are represented by semi-aquatic mammals (Fig. 7). Higher costs are incurred by these semi-aquatic mammals because of thermoregulation in a highly thermally conductive medium, the inefficient drag-based swimming mode and increased drag due to wave formation when swimming at the surface (Fish, 1982, 1992, 1996; Williams, 1983a,b, 1989, 1998; Baudinette and Gill, 1985; Videler and Nolet, 1990).

On the basis of the prediction equations of COT_{min} versus body mass for running and surface-swimming mammals reported by Williams (1998), the lowest value of COT for running *H. chrysogaster* was higher than predicted by 1.7-fold, whereas COT_{min} for swimming was 10% lower than predicted (Fig. 7). Previous work by Dawson and Fanning (1981) on *H. chrysogaster* swimming at approximately 0.3 m s^{-1} in water at 25°C provided a COT of $4.46 \text{ J N}^{-1} \text{ m}^{-1}$. This value, which was probably not COT_{min} , was 1.2 times greater than the COT_{min} from the present study and 1.5 times the predicted value. The COT data for running and swimming demonstrate high relative costs for both methods of locomotion. Although COT_{min} for swimming was lower than predicted, the cost was over 10-fold higher compared with that of a swimming fish of equal mass (Williams, 1998).

COT_{min} for swimming *H. chrysogaster* was close to the value reported for swimming muskrat (Fig. 7; Fish, 1982). In addition to similar effects from surface swimming, the close agreement of these physiological data may indicate similarities due to environment, phylogenetic affinities and swimming mode (Huey, 1987; Fish, 1992). Both muskrat and water rat are members of the rodent family Muridae, and they live in habitats associated with streams, rivers, lakes, marshes and estuaries (Nowak, 1991; Strahan, 1995). Both animals dive and show similar thermoregulatory responses to exposure to cold water (Fish, 1979; Dawson and Fanning, 1981; MacArthur, 1984). The muskrat, like the water rat, swims by alternate paddling strokes of the hindlimbs (Fish, 1984).

The mink, a mustelid, had a substantially higher COT_{min} than swimming *H. chrysogaster*. Mink use a quadrupedal paddling mode that is considered to be primitive and inefficient compared with hindlimb bipedal paddling (Williams, 1983a; Fish, 1992, 1993a). The low swimming costs (Fig. 7) of the beaver (*Castor canadensis*), the river otter (*Lutra lutra*), the sea otter (*Enhydra lutris*) and the platypus (*Ornithorhynchus anatinus*) arise because of submerged swimming and the use of high-efficiency undulatory and lift-based swimming modes (Williams, 1989; Fish, 1996; Allers and Culik, 1997; Fish et al., 1997; Pfeiffer and Culik, 1998). Sea otters can lower their total swimming cost by 69% by subsurface swimming using undulatory propulsive movements rather than paddling at the surface. The additive influence of surface effects and swimming mode was also demonstrated for ducks and penguins (Baudinette and Gill, 1985). The little penguin (*Eudyptula minor*) reduced its oxygen consumption by approximately 30% by submerged swimming. Further reduction in swimming cost for the penguin was noted when compared with paddling ducks (*Anas superciliosa*), because of its use of subaqueous flight. In this type of swimming, the propulsive appendages are modified as high-aspect-ratio hydrofoils that generate thrust almost continuously through the

Fig. 7. Minimum cost of transport (COT_{min}) versus body mass. Blue symbols represent COT_{min} values for paddling semi-aquatic and terrestrial mammals when surface swimming, red symbols represent semi-aquatic and terrestrial running COT_{min} values, and black symbols represent submerged swimming by semi-aquatic mammals. Data are from Fish (1982), Williams (1983a,b, 1989), DiPrampero (1986), Allers and Culik (1997), Fish et al. (1997) and Pfeiffer and Culik (1998). The solid lines represent the extrapolated COT_{min} for semi-aquatic paddlers (blue; $COT=26.81U^{-0.18}/9.8$), runners (red; $COT=10.7U^{-0.32}/9.8$), marine mammals swimming submerged (black; $COT=7.79U^{-0.29}/9.8$) and submerged swimming fish (green; $2.15U^{-0.25}/9.8$) from Williams (1998).



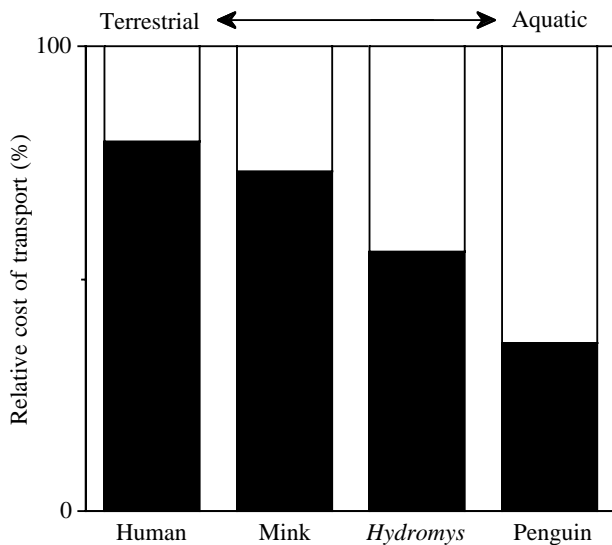


Fig. 8. Relative cost of transport for running (open columns) and swimming (filled columns) terrestrial (human, mink), semi-aquatic (water rat *Hydromys chrysogaster*) and aquatic (penguin) animals.

stroke cycle (Webb, 1975; Baudinette and Gill, 1985; Fish, 1993a, 1996).

The difference in COT between swimming and running by the semi-aquatic *H. chrysogaster* was relatively small compared with that for animals towards the extremes of the terrestrial–aquatic continuum (Fig. 7). Swimming COT_{min} was only 1.25 times greater than the lowest COT for running (Fig. 8). Humans, representing fully terrestrial species, are relatively poor swimmers, with a swimming cost approximately four times as great as the running cost (DiPrampero, 1986) (Fig. 8). Although terrestrial locomotion is more energetically costly for humans than predicted (Fig. 7), the cost of swimming is 22.5 times greater than COT_{min} for a fish of equivalent size (Fig. 7). Consideration of mink as more terrestrial in its habits than the water rat is validated with swimming COT_{min} equal to 2.73 times running COT_{min} (Fig. 8; Williams, 1983a,b). At the opposite end of the continuum is the aquatic penguin, which can move on land with an expensive (1.8 times the predicted value) bipedal waddling gait (Pinshow et al., 1977; Baudinette and Gill, 1985). COT_{min} for walking is 1.8 times greater than swimming costs (Fig. 8).

Evolutionary implications

The reversal in energetic cost of locomotion along the terrestrial–aquatic continuum coincides with a suite of adaptations that enhance locomotor performance with a more aquatic lifestyle. The evolution of increased aquatic habits in many mammals necessitated modification of the propulsive appendages from weight-bearing, inverted pendular struts to large-surface-area paddles or hydrofoils for accelerating a large mass of water (Alexander, 1991; Fish, 1993a, 1996; Thewissen and Fish, 1997). In the specific case of the evolution of cetaceans and sirenians, the limbs digressed and were

abandoned or relegated to function as stabilizing control surfaces with the tail, which acts as the propulsor (Gingerich et al., 1990, 1994; Thewissen and Fish, 1997; Zimmer, 1998). This change in limb structure would impact negatively on the energetics of the performance of an aquatic mammal on land, although performance in the water would be enhanced.

Pinnipeds (e.g. seals, sea lions, walrus) are highly derived aquatic mammals that periodically locomote on land (English, 1976; Gordon, 1981; Feldkamp, 1987; Fish et al., 1988). Their limbs have been modified as flippers. During swimming, these flippers are used as hydrofoils to generate thrust at high efficiency and low COT (Davis et al., 1985; Williams and Kooyman, 1985; Feldkamp, 1987; Fish et al., 1988). Swimming COT_{min} for harbor seals (*Phoca vitulina*) and sea lions was 2.4–4 times greater than that for similarly sized fish (Davis et al., 1985; Feldkamp, 1987). While no comparable data exist for pinnipeds moving on land, energy economy during terrestrial locomotion appears to be sacrificed because of the morphological specialization for swimming. In commercial kills of fur seals (*Callorhinus ursinus*), males were herded inland 0.4–1.2 km at a leisurely pace (Bartholomew and Wilke, 1956; Irving et al., 1962). Despite an air temperature of less than 10 °C, these fur seals occasionally died from heat exhaustion (Bartholomew and Wilke, 1956). Indeed, even on cold damp mornings, fur seals would have started panting before traveling 45 m.

During static exercise experiments in which horses and dolphins swim while pulling or pushing on a load cell, respectively, performance differences between these opposite poles of the terrestrial–aquatic continuum become apparent (Thomas et al., 1980; Goforth, 1990). Horses are highly adapted cursors capable of load-carrying, running at high speed and jumping, but their morphology accentuating terrestrial locomotion makes them poor swimmers. Horses were able to exert a maximum force of 45 kg while swimming in place for 5 min (Thomas et al., 1980). This was equal to a ratio of force to body mass of 0.08. The rates of oxygen consumption and lactic acid production both began to increase at a force level of 0.04 times body mass (Thomas et al., 1980). However, dolphins (*Tursiops truncatus*) were able to produce maximum forces during static swimming of 1.08–1.56 times body mass and forces of 0.3–0.6 times body mass at maximum oxygen consumption with minimum lactate production (Goforth, 1990; Williams et al., 1993). However for dolphins, terrestrial locomotion is virtually impossible.

The intermediate position of semi-aquatic mammals in the terrestrial–aquatic continuum results in greater locomotor costs owing to their inability to specialize in either environment. Williams (1998) argued that mammals had to vault an ‘energetic hurdle’ encountered during the semi-aquatic state in the evolution from terrestrial specialists to aquatic specialists. Transport costs for these locomotor specialists are similar to each other and lower than for semi-aquatic mammals (Fig. 8). To overcome the locomotor inefficiency, semi-aquatic mammals would have compensated by exploiting increased energy resources (Williams, 1998).

Besides the platypus, *H. chrysogaster* is the only other semi-aquatic mammal on the entire continent of Australia. With its habits as an aquatic predator (Troughton, 1941), *H. chrysogaster* has exploited an energetically rich niche left vacant by the endemic marsupials.

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References

- Aigeldinger, T. L. and Fish, F. E.** (1995). Hydroplaning by ducklings: overcoming limitations to swimming at the water surface. *J. Exp. Biol.* **198**, 1567–1574.
- Alexander, R. McN.** (1988). Why mammals gallop. *Am. Zool.* **28**, 237–245.
- Alexander, R. McN.** (1991). Energy-saving mechanisms in walking and running. *J. Exp. Biol.* **160**, 55–69.
- Allers, D. and Culik, B. M.** (1997). Energy requirements of beavers (*Castor canadensis*) swimming underwater. *Physiol. Zool.* **70**, 456–463.
- Barrow, G. J.** (1964). *Hydromys chrysogaster* – some observations. *Queensl. Nat.* **17**, 43–44.
- Bartholomew, G. A. and Wilke, F.** (1956). Body temperature in the Northern fur seal, *Callorhinus ursinus*. *J. Mammal.* **37**, 327–337.
- Baudinette, R. V. and Gill, P.** (1985). The energetics of ‘flying’ and ‘paddling in water: locomotion in penguins and ducks. *J. Comp. Physiol.* **155**, 373–380.
- Bennett, M. B., Ker, R. F. and Alexander, R. McN.** (1987). Elastic properties of structures in the tails of cetaceans (*Phocaena* and *Lagenorhynchus*) and their effect on the energy cost of swimming. *J. Zool., Lond.* **211**, 177–192.
- Blickhan, R. and Cheng, J. Y.** (1994). Energy storage by elastic mechanisms in the tail of large swimmers – a re-evaluation. *J. Theor. Biol.* **168**, 315–321.
- Clark, B. D. and Fish, F. E.** (1994). Scaling of the locomotory apparatus and paddling rhythm in swimming mallard ducklings (*Anas platyrhynchos*): Test of a resonance model. *J. Exp. Zool.* **270**, 245–254.
- Culik, B. M., Wilson, R. P. and Bannasch, R.** (1994). Underwater swimming at low energetic cost by pygoscelid penguins. *J. Exp. Biol.* **197**, 65–78.
- Davis, R. W., Williams, T. M. and Kooyman, G. L.** (1985). Swimming metabolism of yearling and adult harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 590–596.
- Dawson, T. J. and Fanning, F. D.** (1981). Thermal and energetic problems of semi-aquatic mammals: A study of the Australian water rat, including comparisons with the platypus. *Physiol. Zool.* **54**, 285–296.
- DiPrampero, P. E.** (1986). The energy cost of human locomotion on land and in water. *Int. J. Sports Med.* **7**, 55–72.
- English, A. W.** (1976). Limb movements and locomotor function in the California sea lion (*Zalophus californianus*). *J. Zool., Lond.* **178**, 341–364.
- Estes, J. A.** (1989). Adaptations for aquatic living by carnivores. In *Carnivore Behavior, Ecology and Evolution* (ed. J. L. Gittleman), pp. 242–282. Ithaca, NY: Cornell University Press.
- Farley, C. T. and Taylor, C. R.** (1991). A mechanical trigger for the trot–gallop transition in horses. *Science* **253**, 306–308.
- Feldkamp, S. D.** (1987). Swimming in the California sea lion: morphometrics, drag and energetics. *J. Exp. Biol.* **131**, 117–135.
- Fish, F. E.** (1979). Thermoregulation in the muskrat (*Ondatra zibethicus*): the use of regional heterothermia. *Comp. Biochem. Physiol.* **64**, 391–397.
- Fish, F. E.** (1982). Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiol. Zool.* **55**, 180–189.
- Fish, F. E.** (1984). Mechanics, power output and efficiency of the swimming muskrat (*Ondatra zibethicus*). *J. Exp. Biol.* **110**, 183–201.
- Fish, F. E.** (1992). Aquatic locomotion. In *Mammalian Energetics: Interdisciplinary Views of Metabolism and Reproduction* (ed. T. E. Tomasi and T. H. Horton), pp. 34–63. Ithaca, NY: Cornell University Press.
- Fish, F. E.** (1993a). Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Aust. J. Zool.* **42**, 79–101.
- Fish, F. E.** (1993b). Comparison of swimming kinematics between terrestrial and semi-aquatic opossums. *J. Mammal.* **74**, 275–284.
- Fish, F. E.** (1996). Transitions from drag-based to lift-based propulsion in mammalian swimming. *Am. Zool.* **36**, 628–641.
- Fish, F. E., Baudinette, R. V., Frappell, P. B. and Sarre, M. P.** (1997). Energetics of swimming by the platypus *Ornithorhynchus anatinus*: metabolic effort associated with rowing. *J. Exp. Biol.* **200**, 2647–2652.
- Fish, F. E., Innes, S. and Ronald, K.** (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157–173.
- Fish, F. E. and Stein, B. R.** (1991). Functional correlates of differences in bone density among terrestrial and aquatic genera in the family Mustelidae (Mammalia). *Zoomorph.* **110**, 339–345.
- Full, R. J.** (1989). Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. In *Energy Transformations in Cells and Animals* (ed. W. Wieser and E. Gnaiger), pp. 175–182. Stuttgart: Thieme.
- Gingerich, P. D., Raza, S. M., Arif, M., Anwar, M. and Zhou, X.** (1994). New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Science* **368**, 844–847.
- Gingerich, P. D., Smith, B. H. and Simons, E. L.** (1990). Hind limbs of Eocene *Basilosaurus*: Evidence of feet in whales. *Science* **249**, 154–157.
- Goforth, H. W.** (1990). Ergometry (exercise testing) of the bottlenose dolphin. In *The Bottlenose Dolphin* (ed. S. Leatherwood), pp. 559–574. New York: Academic Press.
- Gordon, K. R.** (1981). Locomotor behaviour of the walrus (*Odobenus*). *J. Zool., Lond.* **195**, 349–367.
- Grant, T. R. and Dawson, T. J.** (1978). Temperature regulation in the platypus, *Ornithorhynchus anatinus*: Production and loss of metabolic heat in air and water. *Physiol. Zool.* **51**, 315–332.
- Heglund, N. C. and Taylor, C. R.** (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301–318.
- Heglund, N. C., Taylor, C. R. and McMahon, T. A.** (1974). Scaling stride frequency and gait to animal size: Mice to horses. *Science* **186**, 1112–1113.
- Hertel, H.** (1966). *Structure, Form, Movement*. New York: Reinhold Publishing Co.

- Hildebrand, M.** (1976). Analysis of tetrapod gaits: General considerations and symmetrical gaits. In *Neural Control of Locomotion* (ed. R. M. Herman, S. Grillner, P. S. G. Stein and D. G. Stuart), pp. 203–236. New York: Plenum Press.
- Hildebrand, M.** (1980). The adaptive significance of tetrapod gait selection. *Am. Zool.* **20**, 255–267.
- Hoerner, S. F.** (1965). *Fluid-Dynamic Drag*. Brick Town, NJ: Published by the author.
- Holmér, I.** (1972). Oxygen uptake during swimming in man. *J. Appl. Physiol.* **33**, 502–509.
- Holmér, I. and Åstrand, P.-O.** (1972). Swimming training and maximal oxygen uptake. *J. Appl. Physiol.* **33**, 510–513.
- Howell, A. B.** (1930). *Aquatic Mammals*. Springfield, IL: Charles C. Thomas.
- Hoyt, D. F. and Taylor, C. R.** (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.
- Huey, R. B.** (1987). Phylogeny, history and the comparative method. In *New Directions in Ecological Physiology* (ed. M. E. Feder, A. F. Bennett, W. W. Burggren and R. B. Huey), pp. 76–101. Cambridge: Cambridge University Press.
- Irving, L., Peyton, L. J., Bahn, C. H. and Peterson, R. S.** (1962). Regulation of temperature in fur seals. *Physiol. Zool.* **35**, 275–284.
- Lang, T. G. and Daybell, D. A.** (1963). Porpoise performance tests in a seawater tank. *Nav. Ord. Test Sta. Tech. Rep.* **3063**, 1–50.
- Liu, P. and Bose, N.** (1993). Propulsive performance of three naturally occurring oscillating propeller planforms. *Ocean Eng.* **20**, 57–75.
- Long, J. H., Jr, Pabst, D. A., Shepherd, W. R. and McLellan, W. A.** (1997). Locomotor design of dolphin vertebral columns: bending mechanics and morphology of *Delphinus delphis*. *J. Exp. Biol.* **200**, 65–81.
- MacArthur, R. A.** (1984). Aquatic thermoregulation in the muskrat (*Ondatra zibethicus*): energy demands of swimming and diving. *Can. J. Zool.* **62**, 241–248.
- Marchaj, C. A.** (1964). *Sailing Theory and Practice*. New York: Dodd, Mead & Co.
- Mordvinov, Y. E.** (1976). Locomotion in water and the indices of effectiveness of propelling systems for some aquatic mammals. *Zool. Zh.* **55**, 1375–1382 (in Russian).
- Nadel, E. H.** (1977). Thermal and energetic exchanges during swimming. In *Problems with Temperature Regulation during Exercise* (ed. E. H. Nadel), pp. 91–119. New York: Academic Press.
- Nowak, R. M.** (1991). *Walker's Mammals of the World*. Baltimore: Johns Hopkins University Press.
- Pabst, D. A.** (1996). Springs in swimming animals. *Am. Zool.* **36**, 723–735.
- Pfeiffer, P. and Culik, B. M.** (1998). Energy metabolism of underwater swimming in river-otters (*Lutra lutra* L.). *J. Comp. Physiol. B* **168**, 143–148.
- Pinshow, B., Fedak, M. A. and Schmidt-Nielsen, K.** (1977). Terrestrial locomotion in penguins: It costs more to waddle. *Science* **195**, 592–594.
- Prange, H. and Schmidt-Nielsen, K.** (1970). The metabolic cost of swimming in ducks. *J. Exp. Biol.* **53**, 763–777.
- Schmidt-Nielsen, K.** (1972). Locomotion: Energy cost of swimming, flying and running. *Science* **177**, 222–228.
- Sokolov, V. E.** (1982). *Mammal Skin*. Berkeley: University of California Press.
- Stein, B. R.** (1981). Comparative limb myology of two opossums, *Didelphis* and *Chironectes*. *J. Morph.* **169**, 113–140.
- Strahan, R.** (1995). *The Mammals of Australia*. Chatswood, NSW: Reed Books.
- Tarasoff, F. J., Bisailon, A., Pierard, J. and Whitt, A. P.** (1972). Locomotory patterns and external morphology of the river otter, sea otter and harp seal (Mammalia). *Can. J. Zool.* **50**, 915–929.
- Taylor, C. R.** (1978). Why change gaits? Recruitment of muscles and muscle fibers as a function of speed and gait. *Am. Zool.* **18**, 153–161.
- Taylor, C. R.** (1985). Force development during sustained locomotion: A determinant of gait, speed and metabolic power. *J. Exp. Biol.* **115**, 253–262.
- Taylor, D. W.** (1933). *The Speed and Power of Ships*. Washington, DC: Ransdell Inc.
- Thewissen, J. G. M. and Fish, F. E.** (1997). Locomotor evolution in the earliest cetaceans: Functional model, modern analogues and paleontological evidence. *Paleobiol.* **23**, 482–490.
- Thomas, D. P., Fregin, G. F., Gerber, N. H. and Ailes, N. B.** (1980). Cardiorespiratory adjustments to tethered-swimming in the horse. *Pflügers Arch.* **385**, 65–70.
- Troughton, E.** (1941). Australian water-rats: Their origin and habits. *Aust. Mus. Mag.* **7**, 377–381.
- Tucker, V. A.** (1970). Energetic cost of locomotion in animals. *Comp. Biochem. Physiol.* **34**, 841–846.
- Tucker, V. A.** (1975). The energetic cost of moving about. *Am. Sci.* **63**, 413–419.
- Videler, J. J.** (1993). *Fish Swimming*. London: Chapman & Hall.
- Videler, J. J. and Nolet, B. A.** (1990). Cost of swimming measured at optimum speed: Scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. *Comp. Biochem. Physiol.* **97A**, 91–99.
- Vogel, S.** (1981). *Life in Moving Fluids*. Boston: Willard Grant Press.
- Webb, P. W.** (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–158.
- Webb, P. W., Sims, D. and Schultz, W. W.** (1991). The effects of air/water surface on the fast-start performance of rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **155**, 219–226.
- Williams, T. M.** (1983a). Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. *J. Exp. Biol.* **103**, 155–168.
- Williams, T. M.** (1983b). Locomotion in the North American mink, a semi-aquatic mammal. II. The effect of an elongate body of running energetics and gait patterns. *J. Exp. Biol.* **105**, 283–295.
- Williams, T. M.** (1989). Swimming by sea otters: adaptations for low energetic cost locomotion. *J. Comp. Physiol. A* **164**, 815–824.
- Williams, T. M.** (1998). The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Phil. Trans. R. Soc. B* (in press).
- Williams, T. M., Friedl, W. A. and Haun, J. E.** (1993). The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. *J. Exp. Biol.* **179**, 31–46.
- Williams, T. M. and Kooyman, G. L.** (1985). Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 576–589.
- Withers, P. C.** (1977). Measurement of $\dot{V}O_2$, $\dot{V}CO_2$, and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* **42**, 120–123.
- Woollard, P., Vestjens, W. J. M. and MacLean, L.** (1978). The ecology of the eastern water rat *Hydromys chrysogaster* at Griffith, N.S.W.: food and feeding habits. *Aust. Wildl. Res.* **5**, 59–74.
- Zimmer, C.** (1998). *At the Water's Edge*. New York: Free Press.