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Comparative Biochemistry and Physiology Part A 133 (2002) 203–212

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Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land?[☆]

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Received 11 June 2001; received in revised form 5 May 2002; accepted 7 May 2002

Abstract

Semi-aquatic mammals move between two very different media (air and water), and are subject to a greater range of physical forces (gravity, buoyancy, drag) than obligate swimmers or runners. This versatility is associated with morphological compromises that often lead to elevated locomotor energetic costs when compared to fully aquatic or terrestrial species. To understand the basis of these differences in energy expenditure, this study examined the interrelationships between limb morphology, cost of transport and biomechanics of running in a semi-aquatic mammal, the North American river otter. Oxygen consumption, preferred locomotor speeds, and stride characteristics were measured for river otters (body mass = 11.1 kg, appendicular/axial length = 29%) trained to run on a treadmill. To assess the effects of limb length on performance parameters, kinematic measurements were also made for a terrestrial specialist of comparable stature, the Welsh corgi dog (body mass = 12.0 kg, appendicular/axial length = 37%). The results were compared to predicted values for long legged terrestrial specialists. As found for other semi-aquatic mammals, the net cost of transport of running river otters ($6.63 \text{ J kg}^{-1} \text{ min}^{-1}$ at 1.43 m s^{-1}) was greater than predicted for primarily terrestrial mammals. The otters also showed a marked reduction in gait transition speed and in the range of preferred running speeds in comparison to short dogs and semi-aquatic mammals. As evident from the corgi dogs, short legs did not necessarily compromise running performance. Rather, the ability to incorporate a period of suspension during high speed running was an important compensatory mechanism for short limbs in the dogs. Such an aerial period was not observed in river otters with the result that energetic costs during running were higher and gait transition speeds slower for this versatile mammal compared to locomotor specialists.

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Keywords: Cost of transport; Stride frequency; Corgi dog; River otter; Limb length; Energetics; Running

[☆] This paper was presented in the session, 'Physiology and Biochemistry of Exercise', at the Society for Experimental Biology, April 2–6, 2001, Canterbury, UK.

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1. Introduction

As intermediaries between the terrestrial and aquatic environment, semi-aquatic birds and mammals face physiological challenges rarely encountered by specialists. Water is 800 times denser and 60 times more viscous than air, making locomotor movements comparatively more difficult in water. Primary forces that govern aquatic locomotion are drag and buoyancy, and for deep diving animals hydrostatic pressure (Williams, 2001; Denny, 1993). This contrasts markedly with locomotion on land in which gravitational forces acting on the body represent the major physical factor to be overcome. A consequence of the disparate physical properties of air and water are very different forms of locomotion for runners and swimmers (Dejours, 1987). Despite the apparent difficulties associated with accommodating the mechanics of running and swimming, semi-aquatic species routinely engage in both activities.

The energetic costs associated with swimming by semi-aquatic animals can be exceptionally high depending on the degree of aquatic adaptation. As a group, semi-aquatic birds and mammals swimming on the water surface show some of the highest transport costs measured to date. The total cost of transport for swimming by semi-aquatic mammals is 2.4–5.1 times greater than found for swimming marine mammals (Williams, 1999). When compared to transport costs for swimming fish, the differences are even greater, with semi-aquatic birds and mammals showing transport costs that are 10–25 times higher than predicted for comparably sized fish (Schmidt-Nielsen, 1972). These differences in swimming transport costs between semi-aquatic animals and swimming specialists have been attributed to drag associated with a surface or submerged position (Williams, 1989), and to the efficiency of the propulsive mechanism (Fish, 1993, 1996, 2000). Inherent in the latter is the design of the animal for one or more than one form of locomotion. Animals such as Eurasian otters (*Lutra lutra*; Pfeiffer and Culik, 1998), American mink (*Mustela vison*; Williams, 1983), muskrats (*Ondatra zibethicus*; Fish, 1982), water rats (*Hydromys chrysogaster*; Fish and Baudinette, 1999) and penguins (*Eudyptula minor*; Baudinette and Gill, 1985) that move both on land and in water show elevated costs of transport for swimming in comparison to locomotor specialists.

The relationships between morphological specialization, and the biomechanics and energetic costs of running by semi-aquatic animals are less clear. Earlier studies on the American mink reported little difference in stride frequency or stride length at the trot–gallop transition speed between mink and similarly sized terrestrial mammals (Williams, 1983). The resulting cost of transport for running mink was higher than predicted for running specialists (Taylor et al., 1982). Similar results are reported by Fish and Baudinette (1999) for running Australian water rats. The cost of transport for walking by a semi-aquatic bird such as the penguin is even higher than observed for these semi-aquatic mammals, approaching twice that predicted for similarly sized terrestrial mammals (Pinshow et al., 1977). Recently, these elevated costs have been attributed to the comparatively short legs of the birds (Griffin and Kram, 2000).

The general conclusion from these previous studies is that compromises in body morphology to accommodate two forms of locomotion (swimming and running) often lead to elevated energetic costs of transport in semi-aquatic birds and mammals. To understand the basis of these elevated costs when moving on land, we examined the kinematics and energetics of running in the North American river otter (*Lontra canadensis*). This mammal was chosen because of its reported locomotor proficiency on land and in water (Fish, 1994, 2000; Kruuk, 1995). Measurements included oxygen consumption during running, gait characteristics and preferred speeds. The effects of limb length on performance characteristics were assessed by comparing gait transition speeds and maximum running speeds for river otters to a terrestrial specialist of similar size and body structure, the Pembroke Welsh Corgi dog (*Canis familiaris*). Kinematic data for both the river otters and corgi dogs were then compared to predictions for long legged, terrestrial mammals. Lastly, we compared the data on running energetics of the otters to previously reported values for aquatic and terrestrial specialists as well as other semi-aquatic mammals.

2. Materials and methods

2.1. Animals

Morphological characteristics of the animals used in this study are presented in Table 1. Fifteen

Table 1
Morphological characteristics of the river otters and dogs in this study

	Body mass (kg)	Body length (m)	Appendicular/axial length
<i>River otters</i>			
Male ($n=10$)	11.1±0.7	0.90	0.29
<i>Corgi dogs</i>			
Female ($n=1$)	13.2	0.80	0.35
Male ($n=1$)	12.2	0.75	0.39

Body length was the straight line measurement from the nose to the base of the tail. Height at the shoulders when standing was used as an index of appendicular length. Mean values for adult animals are presented.

North American river otters had been captured from northwestern Prince William Sound, Alaska and flown to the Alaska SeaLife Center (Seward, AK) for a companion study (Ben-David et al., 2000). Locomotor studies on 10 of the captive otters were conducted after a 5-month acclimation period in the facility.

Details of the capture methods, housing, and diet are reported elsewhere (Ben-David et al., 2000). Briefly, river otters were housed as a single group in outdoor pens surrounding one large salt-water pool (4.5 m diameter×3 m deep) and five additional smaller pools (1 fresh water, 4 salt water). Otters were fed daily on a diet of fish supplemented with vitamins. All otters were released at the site of capture following completion of the studies.

To determine if short stature was the primary factor affecting performance in river otters, we also conducted kinematic studies on a similarly sized 'short' dog, the Pembroke Welsh corgi. Two adult Welsh corgis from a local breeder were used in the studies. Dogs were housed in indoor–outdoor kennels and fed daily on a diet of dog chow supplemented with vitamins.

2.2. Oxygen consumption

The rate of oxygen consumption (\dot{V}_{O_2}) was determined for river otters at rest and during running on a motorized treadmill. Each animal was trained over several months to run in a Plexiglas chamber (54 cm high×31 cm wide×138 long) mounted over the treadmill surface. Resting measurements were made on sedentary animals prior to the exercise tests. Oxygen consumption was determined using an open flow respirometry

system as in Williams (1983) and Ben-David et al. (2000). Air was drawn in along the lower edge of the chamber with a vacuum pump (Sears 2.0 Hp Wet/Dry Vac) at flow rates averaging 61–64 l min⁻¹. Flow rates were maintained at levels to ensure that oxygen levels in the chamber remained above 20% during the tests, and were monitored continuously with a calibrated dry gas flow meter (American Meter Co., Inc., DTM-325; San Leandro, CA). Expired air was removed through a port located on the top of the metabolic chamber and samples dried (Drierite) and scrubbed of CO₂ (Sodasorb) before entering the oxygen analyzer (AEI Technologies S3-A; Pittsburgh, PA). The percentage of oxygen in the exhaust air was monitored continuously during the experiments, and recorded with a personal computer using Sable Systems Software (Salt Lake City, UT). The output from the oxygen analyzer was monitored every second and averaged for each minute. These values were converted to \dot{V}_{O_2} using equations modified from Fedak et al. (1981) and Withers (1977) assuming a respiratory quotient of 0.77. All values were corrected to standard temperature and pressure, dry. The entire system was calibrated daily with dry ambient air (20.94% O₂) and nitrogen gas (100% N₂) using the nitrogen dilution techniques of Fedak et al. (1981). The theoretical fraction of O₂ leaving the chamber was calculated (Davis et al., 1985) and compared to the measured values from the oxygen analyzer. The flow of calibration gases into the dome was controlled and monitored by an electronic flowmeter (Omega, Model #FMA-772V) that was accurate to within 1%. Calibrations of the flowmeter were conducted with nitrogen gas and a rotameter (Cole-Palmer Instruments) before and after the studies.

All respirometry experiments were conducted outdoors at $T_{air}=2.9$ – 9.4 °C, which prevented the exercising otters from becoming overheated. On each experimental day, an otter was placed in the metabolic chamber and allowed to rest for approximately 10–15 min. Following the rest period the treadmill was started and the speed increased until the desired test speed was reached. Percentage oxygen was monitored continuously. Otters maintained a forward position in the front of the chamber during the tests. Each animal ran for 10–20 min and was 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 otters were

released from the chamber and allowed to join the rest of the group in the enclosure. Only one speed was tested on any experimental day. The range of test speeds was determined by the ability of the otters to maintain a forward position in the front of the chamber and steady gaits. Experiments were terminated if running performance was inconsistent or the otters turned around. All otters were fasted overnight and were post-absorptive at the time of the tests.

2.3. Running kinematics

Running gaits and stride frequency were determined from videotape records of river otters running on a motorized treadmill and corgi dogs running along a 10 m outdoor, gravel test course. Locomotor movements of the running animals were recorded continuously during the tests with a video camera (Sony CCD TR400) mounted on a tripod. The camera was positioned perpendicular to the treadmill or running path of the otters and dogs, respectively. To ensure consistency between methods, a series of treadmill tests were also conducted with the corgi dogs. Stride frequencies determined from treadmill tests and the outdoor course agreed to within 12% over the range of speeds and gaits examined.

Video images were manually digitized at 60 fields per second using a motion analysis system (Peak Performance Technologies, Inc., Englewood, CO). Running gaits of the animals were correlated to speed and stride frequency. For comparative purposes, we assessed stride frequency according to Heglund and Taylor (1988). The timing intervals for sequential cycles of the front right limb were averaged from video sequences of the running animals, and the number of strides taken per second calculated for each gait. These calculated values were compared to stride frequencies determined from digitized video sequences and were found to be accurate to within 10%. Distances used in the determination of speed were calibrated against the measured length of the animals (Table 1) as well as 10-cm markers placed in the background of the test course and treadmill. Timing of the video system was calibrated against a digital clock placed in the field of view.

2.4. Analysis and statistics

Break points in the data for oxygen consumption in relation to running speeds were determined from

the intersection of multiple regressions following the approach of Yeager and Ultsch (1989). Allometric regressions for cost of transport in relation to body mass, and relationships for oxygen consumption versus speed were determined using least squares methods (Sigma-Stat, Jandel Scientific Software, 1995). Remaining data are reported as means \pm 1 S.E.M. unless otherwise indicated.

3. Results

3.1. Oxygen consumption

The mean rate of oxygen consumption for the otters resting in the metabolic chamber was $9.69 \text{ mlO}_2 \text{ kg}^{-1} \text{ min}^{-1} \pm 0.91$ ($n=3$ lowest recordings for 10 otters). This value was within 1.5% of the value reported by Kruuk (1995) for the Eurasian river otter and was 34.4% higher than the predicted value for basal metabolic rate in mustelids (Iverson, 1972). Oxygen consumption increased with running speed and showed two different functions depending on gait (Fig. 1). From rest to 1.2 m s^{-1} oxygen consumption increased linearly with speed as described by

$$\dot{V}_{\text{O}_2} = 14.1 + 23.4 \text{ speed} \\ (n=27 \text{ trials}, r^2=0.76, P<0.001) \quad (1)$$

where \dot{V}_{O_2} is in $\text{mlO}_2 \text{ kg}^{-1} \text{ min}^{-1}$ and speed is in m s^{-1} . Over this range of speeds the river otters used a walking gait. At higher tread speeds the otters switched to a half-bound or bounding gait and showed no relationship between oxygen consumption and bounding speed. Mean \dot{V}_{O_2} during bounding from 1.2 to 1.6 m s^{-1} was 38.01 ± 0.74 ($n=18$ trails).

3.2. Running kinematics

As previously described by Tarasoff et al. (1972), river otters used two primary gaits during the treadmill tests, a walk at slow speeds (0.5 – 1.2 m s^{-1}) and a bound or half-bound at higher speeds. Because the half-bound was used intermittently and overlapped with the range of bounding speeds, data for both gaits were combined and termed 'bound' for the remainder of the analyses. The transition between walking and bounding gaits occurred at 1.2 m s^{-1} .

Stride frequency of running river otters showed

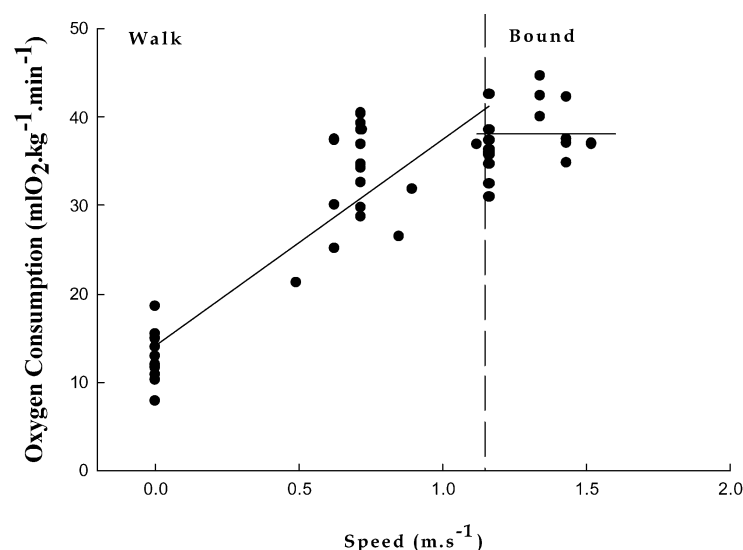


Fig. 1. Oxygen consumption in relation to running speed for river otters. Each point represents a single trial for an individual otter. The solid lines are the least squares linear regression for the walking otters and the mean level for bounding otters, respectively, as described in the text. The vertical dashed line denotes the average gait transition speed for the otters. Data at zero speed is for sedentary otters in the metabolic chamber prior to the exercise session.

two patterns with locomotor speed that depended on gait (Fig. 2a). Over the range of walking speeds stride frequency increased linearly with speed according to the relationship

$$\text{Stride frequency} = 1.06 + 0.68 \text{ speed} \quad (2)$$

($n = 25$ trials, $r^2 = 0.53$, $P < 0.001$)

where stride frequency is in strides s^{-1} and speed is in $m s^{-1}$. In contrast, the frequency of high speed bounding showed no pattern with speed. Mean stride frequency for bounding was 2.08 ± 0.03 ($n = 16$ trials) for the river otters.

Unlike the otters, corgi dogs showed the three distinct gaits typical of running quadrupedal mammals (Heglund et al., 1974; Heglund and Taylor, 1988). At speeds less than $1.1 m s^{-1}$ corgis used a walking gait (Fig. 2b). This was followed by a change to trotting, and finally galloping at speeds greater than $2.2 m s^{-1}$. The range of speeds the animals performed also differed between the otters and dogs. Running speeds ranged from 0.6 to $1.6 m s^{-1}$ in the river otters. In comparison, corgi dogs ran over a range of 0.6 – $7.4 m s^{-1}$.

Stride frequency of the corgi dogs showed two relationships with running speed that depended on the transition between trotting and galloping (Fig. 2b). During walking and trotting stride frequency increased linearly with speed and was described by the equation

$$\text{Stride frequency} = 1.47 + 0.51 \text{ speed} \quad (3)$$

($n = 57$ trials, $r^2 = 0.60$, $P < 0.001$)

where the units are as in Eq. (2). A second linear regression described the relationship between stride frequency and galloping speed:

$$\text{Stride frequency} = 2.28 + 0.30 \text{ speed} \quad (4)$$

($n = 61$ trials, $r^2 = 0.62$, $P < 0.01$)

where the units are as in the previous equations.

4. Discussion

4.1. The effect of body morphology on energetic costs in semi-aquatic mammals

The body morphology of river otters reflects the combined demands of an aquatic and terrestrial lifestyle, and has resulted in river otters being considered 'intermediates' to terrestrial or aquatic specialists (Tarasoff, 1974). As a group, river otters are relatively large (0.5 – $2.0 m$ long depending on species) semi-aquatic carnivores that live on land but forage primarily in water. Movements on land can be extensive, with males in particular covering large ranges (Kruuk, 1995). Several morphological adaptations enable river otters to meet these diverse locomotor demands with the most obvious being spinal flexibility and a reduction in the length of the limbs (Fig. 3). The former is

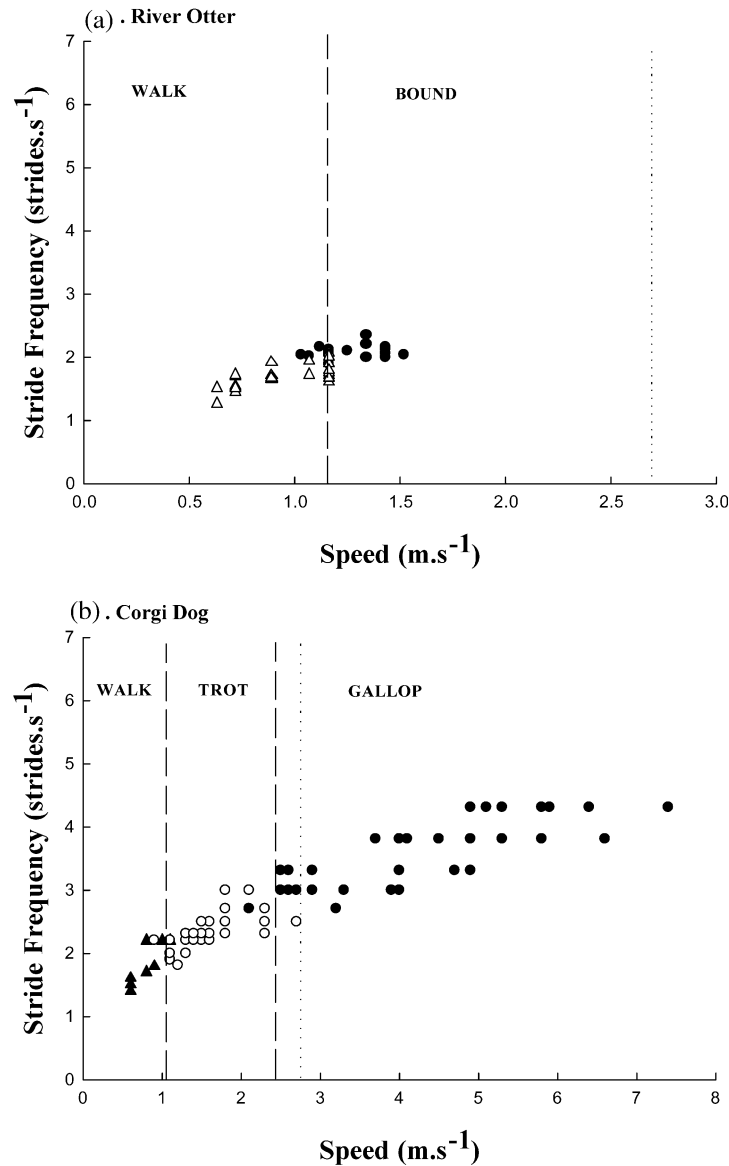


Fig. 2. Stride frequency in relation to running speed for river otters (a); and corgi dogs (b). Each point represents a single exercise trial for an individual animal. Values for walking (open and closed triangles), trotting (open circles), and bounding and galloping (closed circles) are presented. Vertical dashed lines denote the measured transition speed between gaits and vertical dotted lines the predicted trot–gallop speed for quadrupedal mammals (Heglund and Taylor, 1988). Note in particular the difference in the range of locomotor speeds between these similarly sized mammals. Sample size of $n=32$ trials for river otters and 119 trials for dogs.

considered an advantage for dorsoventral bending to power swimming in semi-aquatic (Williams, 1983) and marine (Long et al., 1997) mammals. While long limbs and small plantar (foot) surfaces characterize elite terrestrial runners such as the cheetah, reduced appendicular skeletons and enlarged plantar surfaces are typical of semi-aquatic mammals, the river otter being no excep-

tion (Table 1). The appendicular to axial ratio is 0.29 for the North American river otter, 0.37 for a short-legged dog such as the Welsh corgi, and nearly 0.60 for average proportioned dogs such as the border collie. The benefit of such morphological specialization in semi-aquatic mammals is a streamlined body that produces less hydrodynamic drag during swimming (see Fish, 2000 for a

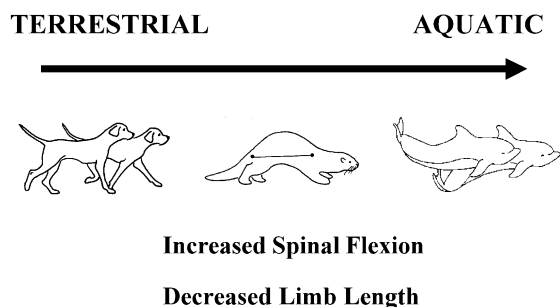


Fig. 3. Relative changes in morphology with the increase in aquatic specialization in mammals. Two major factors affecting terrestrial locomotion in semi-aquatic mammals, an increase in spinal flexion and decrease in limb length, are characteristic of animals designed for an aquatic lifestyle.

review). A potential disadvantage, however, is reduced efficiency when moving on land.

In river otters this disadvantage is manifested as an elevation in the energetic cost of running when compared to the costs of locomotor specialists (Fig. 4). The total cost of transport calculated from the oxygen consumption of bounding river otters (Fig. 1) was $8.90 \text{ J kg}^{-1} \text{ m}^{-1}$. Using basal metabolic rates predicted for river otters from Iverson (1972) we obtain a net cost of transport of $7.21 \text{ J kg}^{-1} \text{ m}^{-1}$. This is reduced to $6.63 \text{ J kg}^{-1} \text{ m}^{-1}$ if the resting metabolic rates obtained in the present study are used in the calculation. The resulting values for net cost of transport are 34–46% greater than predicted for running quadrupedal mammals (Taylor et al., 1982) or swimming marine mammals (Williams, 1999) of similar body mass. Despite the differences in energetic costs between these groups, the elevation in running costs observed for river otters are typical of semi-aquatic mammals. For example, the cost of transport for running North American mink is 25% higher than predicted for terrestrial specialists (Williams, 1983). The Australian water rat demonstrates a minimum cost of running that is 70% higher than predicted values (Fish and Baudinette, 1999).

Fish and Baudinette (1999) have shown that the relative cost of running and swimming for animals correlates with the degree of locomotor specialization. Thus, mammals designed primarily for locomotion on land such as humans have swimming costs that are nearly 4 times that of running (DiPrampero, 1986). At the other extreme of the continuum presented by these investigators is the

penguin, an aquatic bird that has exceptionally high walking costs and a relative cost ratio of only 0.55. As might be expected, semi-aquatic mammals are intermediate to the extremes with swimming cost to running cost ratios of 1.25–2.73. Based on the total cost of running in the present study and the cost of submerged swimming of Eurasian otters from Pfeiffer and Culik (1998), the relative cost ratio for river otters is only 0.17. However, the low ratio for river otters calculated here undoubtedly reflects the effects of submergence on body drag and the physiological responses to diving on the energetic cost of swimming (Williams, 1989). The relative cost ratio for river otters is increased to 1.95, the mid range for semi-aquatic mammals, if the predicted cost of surface swimming (Williams, 1999) is used in the calculation.

Initially, it seems reasonable to attribute the elevated running costs of semi-aquatic mammals to the reduced length of the limbs. This presumes that short limbs will result in shorter stride lengths

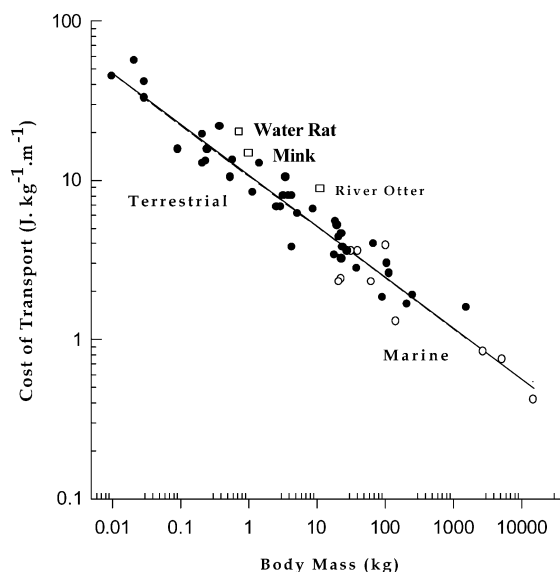


Fig. 4. Cost of transport in relation to body mass for running terrestrial (closed circles), swimming marine (open circles), and running semi-aquatic (open squares) mammals. All animals were considered locomotor specialists except for the water rat, mink, and river otter. The solid line is the least squares regression through the data points. The data and regression represent 29 species of terrestrial specialist and 6 species of marine mammal (from Williams, 1999). Data for the running water rat and mink are from Fish and Baudinette (1999) and Williams (1983), respectively. Cost of transport for the river otter was calculated from the data in Fig. 1.

and a consequent increase in stride frequency to cover a set distance. To test the relationship between limb length and the energetic cost of running, Steudel and Beattie (1995) conducted a phylogenetic analysis for a wide variety of mammals. Their analysis did not find a significant relationship between these variables beyond a 'mutual correlation with body mass'. Kinematic tests on semi-aquatic mammals including the present study support this conclusion. Rather than a compensatory increase in stride frequency, the river otters showed stride frequencies at gait transition speeds that were lower than those predicted for running specialists from Heglund and Taylor (1988). The mean stride frequency at the trot–bound transition speed for river otters, 1.88 ± 0.05 strides s^{-1} ($n=9$), was 36% lower than predicted for the walk–gallop transition of terrestrial mammals (Fig. 2a). Running North American mink (Williams, 1983) and water rats (Fish and Baudinette, 1999) demonstrated less than a 2% difference between predicted and measured stride frequencies at the gait transition.

These results are somewhat misleading due to several compensatory changes in performance by semi-aquatic mammals during high speed running. For a wide range of running mammals, the trot to gallop transition speed changes predictably with body mass (Heglund et al., 1974; Heglund and Taylor, 1988). Based on regressions from these previous studies, the expected gait transition speed for an 11.1 kg river otter is 2.6 m s^{-1} . This compares with the observed walk to bound transition speed of 1.2 m s^{-1} (Fig. 2a), a speed that is less than half of predicted. Other performance characteristics including the range of running speeds and maximum speed were also reduced in the river otters compared to other runners, long- or short-legged (Fig. 2). The maximum running speed for river otters, 1.6 m s^{-1} , was only 35% of the preferred galloping speed predicted for terrestrial mammals of similar body mass and 'normal' body proportions (Heglund and Taylor, 1988). The effect of these shifts in the gait transition and maximum speeds is lower stride frequencies than predicted. Thus, the frequency of limb movements in river otters is comparable or lower than expected, but comes at the expense of the speed of performance.

The question remains, is reduced limb length in semi-aquatic mammals the primary cause of the kinematic and energetic differences observed

between this group and terrestrial specialists? Data for the running corgis suggest that short stature need not be a mechanical hindrance. This breed of dog, similar in body proportions to the river otter, showed gait patterns, stride frequencies and gait transition speeds typical of other terrestrial mammals (Fig. 2b). Unlike the otters (Fig. 2a), the stride frequency of corgis at the trot–gallop transition, 2.9 ± 0.2 strides s^{-1} ($n=5$), was within 4% of the predicted value for terrestrial specialists (Heglund and Taylor, 1988). The primary difference in biomechanics between the otters and corgis was the incorporation of spinal flexion and a period of suspension during high speed running. Galloping corgis, like many other canids, show little spinal flexion but maintain a period of suspension at high speeds (Brown, 1986). Conversely, river otters show a 20.5% decrease in axial length (measured shoulder to hip) and only rarely incorporate an aerial phase during bounding (Scaramozzino, 2000).

Previous studies have suggested that axial flexion during running provides an advantage for increasing speed (Gambaryan, 1974) particularly for semi-aquatic mammals (Williams, 1983). Rather than axial flexion per se, we find that the ability to incorporate a period of suspension during high speed running provides the locomotor advantage for short-legged runners whether or not it is associated with body flexion. Consequently, there is a general trend among semi-aquatic mammals for higher relative costs in those species without a period of suspension during high speed gaits (i.e. water rats, river otters) compared to those with a pronounced aerial phase (i.e. mink, Fig. 4). Likewise, locomotor performance defined in terms of predicted gait transition speeds and range of speeds for short-legged mustelids (Scaramozzino, 2000) and dogs (Fig. 2) is greater in those species that demonstrate a period of suspension during high speed running.

In summary, morphological adaptations to accommodate more than one form of locomotion allows river otters to take advantage of two different environments when hunting. The price of this locomotor versatility includes higher energetic costs during running, and slower gait transition speeds and maximum speeds in comparison to terrestrial specialists. Thus, for the three semi-aquatic mammals tested to date (water rat, mink, and river otter) the energetic cost of both swimming and running are elevated in comparison to

locomotor specialists. The magnitude of the difference between semi-aquatic and terrestrial mammals depends on the degree of morphological specialization.

In addition to basic information on locomotion in semi-aquatic mammals, these results on extant species provide additional insights regarding the physiological and behavioral challenges that may have been encountered as ancestral mammals made the transition from land to sea (Williams, 1999). As body morphology changed to accommodate two forms of locomotion during the transition, the energetic trend would have been from the comparatively low costs of the terrestrial specialist to the comparatively high costs of the semi-aquatic transitional mammal. With improved streamlining and propulsive efficiency, locomotor energetic costs would have decreased to the low cost level of the swimming specialist (Fig. 4). Based on our results for rivers otters, it is likely that ancestral semi-aquatic mammals faced both energetic and performance 'hurdles' during the transition from an obligate terrestrial to an obligate aquatic lifestyle.

Acknowledgments

This study was supported by grants from the Office of Naval Research (N00014-95-1-1023) to T.M. Williams, and the EVOS Trustees Council (project No. 348) and an OWCN grant (UOA97119) to M. Ben-David. The authors thank the many trainers, volunteers and research assistants associated with these studies including P. Tuomi and the entire staff of the Alaska SeaLife Center. In addition, the authors are grateful for the assistance of the many volunteers working in the Williams Physiology Laboratory. All experimental procedures involving animals followed NIH guidelines and were evaluated and approved by individual institutional Animal Use Committees at the University of Alaska Fairbanks and ASLC (#97-14 and 98-002 respectively), and the University of California at Santa Cruz.

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