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The evolution of cost efficient swimming in marine mammals: limits to energetic optimization

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Mammals re-entered the oceans less than 60 million years ago. The transition from a terrestrial to an aquatic lifestyle required extreme morphological and behavioural modifications concomitant with fundamentally different locomotor mechanisms for moving on land and through water. Energetic transport costs typically reflect such different locomotor modes, but can not be discerned from the fossil record. In this study the energetic challenges associated with changing from terrestrial to aquatic locomotion in primitive marine mammals are examined by comparing the transport, maintenance and locomotor costs of extant mammals varying in degree of aquatic specialization. The results indicate that running and swimming specialists have converged on an energetic optimum for locomotion. An allometric expression, $\mathrm{COT_{TOT}} = 7.79\ \mathrm{mass}^{-0.29}$ ($r^2 = 0.83$, $n = 6$ species), describes the total cost of transport in $\mathrm{J\ kg^{-1}\ m^{-1}}$ for swimming marine mammals ranging in size from 21 kg to 15 000 kg. This relation is indistinguishable from that describing total transport costs in running mammals. In contrast, the transitional lifestyle of semi-aquatic mammals, similar to that of ancestral marine mammals, incurs costs that are 2.4–5.1 times higher than locomotor specialists. These patterns suggest that primitive marine mammals confronted an energetic hurdle before returning to costs reminiscent of their terrestrial ancestry, and may have reached an evolutionary limit for energetic optimization during swimming.

Keywords: swimming; energetics; transport cost; marine mammals; locomotor evolution

1. INTRODUCTION

The evolutionary pathway of marine mammals involved transitions from terrestrial specialists to intermediate forms capable of moving both in air and water, and from these intermediate forms to aquatic specialists (Repenning 1976; Berta *et al.* 1989; Thewissen *et al.* 1994). These transitions were associated with morphological, physiological and behavioural modifications to overcome the disparate physical demands of locomotion through two different media. Since water is 800 times denser and 60 times more viscous than air (Dejours 1987) the transition from terrestrial to aquatic locomotion undoubtedly challenged the mechanical and physiological systems of ancestral marine mammals.

Many of the morphological transitions that led to proficiency in the aquatic environment are revealed in the fossil record. Fossil cetaceans (*Ambulocetus natans*) and pinnipeds (the Enaliarctidae, *Potamotherium*) demonstrate transitional forms within these lineages (Repenning 1976; Berta *et al.* 1989; Thewissen 1994; Thewissen *et al.* 1994) and reflect a continuum for locomotor optimization in marine mammals. Common to these ancestral marine mammals was a locomotor apparatus that supported movements on land and in water. For example, the limbs of transitional pinnipeds and cetaceans were more robust than they are in extant species. Flexibility of the axial skeleton in transitional mammals also suggests the capability for undulatory propulsion when submerged. Thus, *Ambulocetus* probably resembled a swimming otter in water and a shuffling sea lion on land (Fordyce & Barnes 1994; Thewissen *et al.* 1994). Likewise, the skeletons of *Potamotherium* (Repenning 1976) and *Enaliarctos mealsi* (Berta *et al.* 1989) indicate both otter-like and seal-like locomotor patterns for archaic pinnipeds.

Despite revelations about locomotor mechanisms, the fossil record has provided little insight into the coincident physiological constraints and challenges that accompanied the transitions in morphology and lifestyle. Differences in the mechanics of running and swimming as well as in the thermal properties of air and water would demand different energetic inputs as mammals evolved into aquatic forms. Here, I examine the energetic consequences of such transitions by comparing maintenance and locomotor costs, and the total cost of transport of extant mammals varying in degree of aquatic specialization. Extant terrestrial, semi-aquatic and marine mammals were considered representative of principal evolutionary hallmarks within marine mammal lineages. A comparison of transport costs for these transitional and specialized groups of mammals provided an opportunity to assess the energetic consequences of evolving aquatic locomotion from terrestrial building blocks. The results from this study indicate that running and swimming specialists have converged on an energetic

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Table 1. *Energetic costs and swimming speeds of mammalian swimmers*

(Oxygen consumption was determined for animals resting water prior to exercise and during steady-state swimming. Measurements on active animals were done as the subjects swam against a water current in a flume or unrestrained in open water. Oxygen consumption ($mlO_2\,kg^{-1}\,min^{-1}$) was converted to metabolic energy (Joules, J) assuming a caloric equivalent of 4.8 kcal per litre of O_2 and a conversion factor of $4.187 \times 10^3\,J\,kcal^{-1}$. Minimum COT_{TOT} was determined from the lowest oxygen consumption during swimming divided by speed. Criteria for data selection from the literature included: (i) use of respirometry methodologies for measuring metabolic rates of resting and active animals; (ii) steady-state metabolic levels during measurements; and (iii) non-diving conditions.)

species	mass (kg)	$\dot{V}O_{2rest}$	$\dot{V}O_{2swim}$	COT_{TOT} ($J\,kg^{-1}\,m^{-1}$)	speed ($m\,s^{-1}$)	method
		($mlO_2\,kg^{-1}\,min^{-1}$)				
semi-aquatic						
muskrat[b]	0.6	14.7	48.0	21.4	0.75	flume
North American mink[c]	1	20.0	97.5	41.1	0.75	flume
sea otter[d] (surface)	20	13.5	29.6	12.6	0.8	flume
(submerged)	20	13.5	17.6	7.4	0.8[a]	flume
human[e] (elite front crawl	80	24.9	30.0	10.5	1.0	flume
(elite breast stroke)	80	24.9	53.1	16.8	1.0	flume
Marine						
California sea lion[f,g,h]	21	—	13.7	2.3	2.0	flume
	23	6.3	22.0	2.8	2.6	flume
	23	6.6	13.0	2.4	1.8	flume
harbour seal[f,i]	32	—	23.6	3.6	2.2	flume
	33	5.1	15.2	3.6	1.4[a]	flume
	63	4.6	9.6	2.3	1.4[a]	flume
grey seal[j]	104	7.7	15.0	3.9	1.3[a]	flume
bottlenose dolphin[g,k]	145	4.6	8.1	1.3	2.1	ocean swim
killer whale[l]	2738	—	—	0.84	3.1	field respiratory
	5153	—	—	0.75	3.1	rates
grey whale[m]	15 000	—	—	0.4	2.1	field respiratory rates

[a] Represents maximum flume speed. Minimum cost of transport speeds based on routine speed of free ranging animals is $1.0\,ms^{-1}$ for submerged sea otters and *ca*. $2.0\,ms^{-1}$ for phocid seals.

[b] Fish 1982.

[c] Williams 1983.

[d] Williams 1989.

[e] Holmer 1972.

[f] Williams *et al*. 1991.

[g] Present study.

[h] Feldkamp 1987.

[i] Davis *et al*. 1985.

[j] Fedak 1986.

[k] Williams *et al*. 1993.

[l] Kriete 1995.

[m] Sumich 1983.

optimum during locomotion that may represent an evolutionary limit for mammals.

2. ASSESSING ENERGETIC COSTS IN SWIMMING MAMMALS

(a) ***Metabolism during rest and activity in water***

Metabolic rates have been determined for a variety of swimming mammals that differ markedly in propulsive style. The range of subjects include marine mammals specialized for aquatic locomotion and semi-aquatic mammals that routinely move both on land and in water (table 1). Maintenance costs (MC) of aquatic mammals are assessed from the rate of oxygen consumption ($\dot{V}O_2$) measured on quiescent animals floating quietly under metabolic hoods or breathing into gas-collection bags. To avoid elevations in metabolism associated with thermoregulation, water temperatures in the metabolic chambers are maintained at routine pool, pen, or ocean temperatures for individual animals (i.e. 12–25 °C for the subjects in table 1). Likewise, metabolic depression coincident with diving responses can be a complicating factor. When resting, semi-aquatic mammals such as minks (Williams 1983), muskrats (Fish 1982) and humans (Holmer 1972) remain on the water surface whereas marine mammals such as seals (Davis *et al.* 1985; Fedak 1986; Williams *et al.* 1991), sea lions (Feldkamp 1987; Williams *et al.* 1991) and dolphins (T. M. Williams, unpublished data) alternate between floating and briefly submerging. The pinnipeds and cetaceans used in the present study submerged for only brief intervals (less than one minute). Therefore, none were considered to be in a diving state. Under these conditions MC includes the energy expended for basal functions as well as endothermy in the alert animal.

Except for cetaceans, the metabolic rates of swimming mammals are often determined on animals trained to swim against a current in a water flume (table 1). Flume dimensions must take into account the frontal area and propulsive movements of each species. In addition, water flows must provide a physiological challenge for the swimmer (Williams 1987). Most of the energetic data for swimming semi-aquatic mammals and smaller marine mammals have been obtained by using open-flow respirometry in conjunction with these flumes. Because most flumes are too small or too slow for studying cetaceans, exercise tests for swimming dolphins, killer whales and grey whales have used several novel approaches. These include measuring physiological parameters while trained bottlenose dolphins follow a moving boat at sea (Williams *et al.* 1993), and calculating metabolic costs from respiratory patterns of free-ranging killer whales (Kriete 1995) and grey whales (Sumich 1983). A critical feature of these methods is the ability to monitor the subjects at preferred steady state velocities as determined from the routine movements of wild animals.

When comparing the energetics of aquatic mammals it is important to distinguish between swimming and diving activities. In the context of this study, swimming refers to transit swimming in which the course of movement is generally in the horizontal direction and the animal has constant access to air. This differs from diving in which the subject undergoes an extended period of apnea and may initiate a suite of physiological changes including bradycardia, peripheral vasoconstriction and metabolic suppression associated with the dive response (Kooyman 1989). The synergistic metabolic effects of diving superimposed on swimming exercise are beyond the scope of the present study. Therefore, transport costs are compared for transit swimmers only.

(b) *Cost of transport and locomotor costs*

Schmidt-Nielsen (1972) defined the energy cost of locomotion as the amount of fuel it takes to transport one unit of body weight over a unit distance. In the literature, 'total mass specific metabolic rate of the exercising animal divided by speed', as well as, '(total mass specific metabolic rate of the exercising animal minus resting mass specific metabolic rate) divided by speed', have been used interchangeably to define the 'cost of transport'. The former describes the energy required by the individual animal to satisfy both maintenance and locomotor demands during exercise while the latter describes the amount of energy required for moving the body and limbs. These are often termed the total cost of transport ($\mathrm{COT_{TOT}}$) and net cost of transport ($\mathrm{COT_{NET}}$), respectively (Schmidt-Nielsen 1972).

Here, I present total cost of transport ($\mathrm{COT_{TOT}}$), maintenance costs (MC), and locomotor costs (LC) for terrestrial, semi-aquatic and marine species, where

$$\mathrm{COT_{TOT}} = \mathrm{MC} + \mathrm{LC}.$$

$\mathrm{COT_{TOT}}$ is calculated by dividing the total metabolic rate of the active animal by locomotor speed. For aquatic mammals, $\mathrm{COT_{TOT}}$ represents the energy expended for transit swimming to distinguish it from diving. The difference between $\mathrm{COT_{TOT}}$ and MC has been termed the locomotor cost, LC (Williams 1989). This value represents the energy expended by animals for swimming performance and is analogous to $\mathrm{COT_{NET}}$ presented for running mammals (Schmidt-Nielsen 1972). To provide a common basis for comparing $\mathrm{COT_{TOT}}$ between animals of different size or form of locomotion (Taylor *et al.* 1970), minimum $\mathrm{COT_{TOT}}$ for each species is presented (Williams 1987). Energetic costs for mammals are then compared with those of flying birds (Tucker 1973), and salmonid (Brett 1964) and thunniform (Dewar & Graham 1994) fishes.

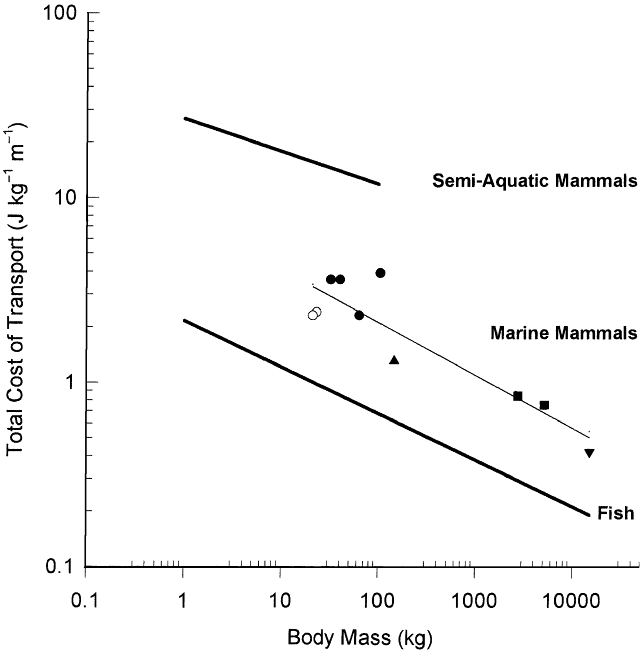

Figure 1. Total cost of transport ($\mathrm{COT_{TOT}}$) in relation to body mass for different classes of swimmers. Individual marine mammals are compared with regressions for semi-aquatic mammals and salmonid fish. Marine mammals include phocid seals (filled circles), California sea lions (empty circles), bottlenose dolphins (upward-pointing triangle), killer whales (squares), and grey whales (downward-pointing triangle) from table 1. The line through the data points is the least squares regression for marine mammals. The lower solid line represents the extrapolated regression for salmonid fish where $y=2.15x^{-0.25}$ (Brett 1964). The upper solid line shows the regression for swimming semi-aquatic mammals from Williams (1989) where $y=26.81x^{-0.18}$ and includes data for North American mink, muskrats, humans and surface-swimming sea otters.

3. DISCUSSION

(a) *Energetic costs incurred by swimmers*

The total cost of transport ($\mathrm{COT_{TOT}}$) for swimming mammals may be separated into two distinct groups distinguished by the degree of locomotor specialization (table 1, figure 1). As might be expected, a transitional lifestyle requiring movement between two media sacrifices energetic efficiency for versatility. Thus, semi-aquatic mammals such as minks and muskrats incur transport costs that are 2.4–5.1 times higher than observed for marine mammals (figure 1). Several factors, including hydrodynamic drag (Williams 1989) and propulsive efficiency (Fish 1993, 1996) undoubtedly contribute to the relatively high swimming costs of semi-aquatic mammals. In particular, elevated body drag associated with a surface-swimming position has a profound effect on transport costs. Theoretically, total drag is 4–5 times higher for a body moving on or near the water surface than for the same body submerged (Hertel 1966). This has been demonstrated for humans and harbour seals (Williams & Kooyman 1985), and sea otters (Williams 1989) by towing subjects on the water surface or submerged. Cardiovascular, respiratory and metabolic responses of swimming seals and sea lions also correspond to the percentage of time that the animal spends on the water surface or submerged while swimming (Williams *et al.* 1991). Similarly, the resulting transport costs for surface and submerged swimming sea otters reflect the differences in body position and drag (table 1).

The total cost of transport is comparatively low in mammals with increased specialization for one form of locomotion. Total transport costs in relation to body mass for swimming marine mammals ranging in size from 21 kg to 15 000 kg is described by

$$\mathrm{COT_{TOT}} = 7.79\,\mathrm{mass}^{-0.29} (r^2 = 0.83, n = 10),$$

where the total cost of transport is in $\mathrm{J\,kg^{-1}\,m^{-1}}$ and body mass is in kilograms. This relation expands the observations of Culik & Wilson (1994) and includes otariid and phocid seals, large and small odontocetes, and a mysticete whale (see figure 1). Swimming style in these animals ranges from dorso–ventral undulation in cetaceans (Fish & Hui 1991) to fore-flipper propulsion in otariids (Feldkamp 1987) and lateral undulation of paired hind flippers in phocid seals (Fish *et al.* 1988). In view of the diversity of propulsive styles, it appears that swimming mode has little effect on $\mathrm{COT_{TOT}}$ among marine mammals. Similar patterns have been reported for other locomotor groups. For example, transport costs do not vary greatly with the style of swimming in fish (Schmidt-Nielsen 1972, 1984; Bennett 1985), or with bipedal or quadrupedal performance in runners (Taylor & Rowntree 1973; Fedak & Seeherman 1979). Among semi-aquatic mammals, a single allometric expression also describes rowers, paddlers and humans performing the front crawl and breaststroke (Williams 1989).

Despite specialization for aquatic locomotion, the $\mathrm{COT_{TOT}}$ of marine mammals are considerably higher than predicted for fish of comparable size (figure 1). Values for pinnipeds including otariids and phocid seals are 2.3–4.0 times those predicted for fish. The $\mathrm{COT_{TOT}}$ of cetaceans ranges from 2.1–2.9 times the predicted values. Bottlenose dolphins show the lowest ratio between measured and predicted values within this range (Williams *et al.* 1993). Larger cetaceans such as the killer whale (Kriete 1995) and grey whale (Sumich 1983) demonstrate $\mathrm{COT_{TOT}}$ that are 2.2–2.9 times those predicted for salmonid fish.

MC, which reflect inherent differences in endothermy between mammals and fish, appear to account for the discrepancy in $\mathrm{COT_{TOT}}$ between these vertebrate groups (figure 2). Endogenous heat production results in a characteristic metabolic disparity between ectotherms and endotherms (Bartholomew 1977). Furthermore, MC for many species of aquatic mammals are exceptionally high owing to the high thermal conductivity of water (Irving 1973; Whittow 1987). Thus, the metabolic rates of many species of aquatic mammal resting in water are 1.7–2.4 times higher than those predicted from allometric regressions for terrestrial mammals resting in air (Kleiber 1975; Williams 1998).

By subtracting the energetic burden of endothermy, we can compare the locomotor costs of marine mammals and fish. In other words, we can compare the amount of energy these animals dedicate to moving their body and appendages through water. This is accomplished by subtracting the MC determined for animals resting in water from its corresponding $\mathrm{COT_{TOT}}$. The resulting LC for many species of pinniped and cetacean resemble those predicted from the allometric relation for salmonid fish (figure 2). Values for sea lions and dolphins are within 11% of predictions; even the sea otter, when swimming submerged, shows LC approaching the expected value for fishes. Adult harbour seals are somewhat higher at 58% over predicted while grey whales are lower by 32%.

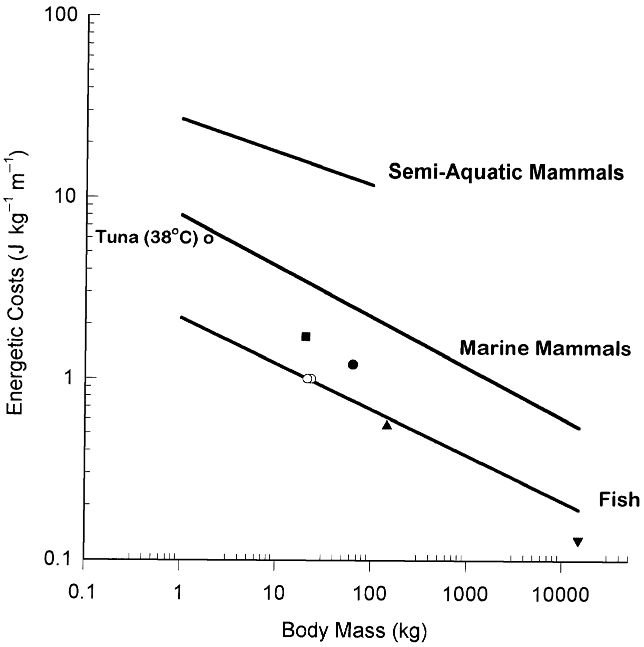

Figure 2. Locomotor costs of marine mammals compared with $\mathrm{COT_{TOT}}$ of different classes of swimmers. Solid lines are the allometric regressions for $\mathrm{COT_{TOT}}$ of semi-aquatic mammals, salmonid fish and marine mammals as in figure 1. Data points represent the mean locomotor costs (LC) for different species of marine mammal including sea otters (square), California sea lions (plain circle), harbour seals (filled circle), bottlenose dolphins (upward-pointing triangle) and grey whales (downward-pointing triangle). Data are from sources cited in figure 1. The calculated $\mathrm{COT_{TOT}}$ for swimming tuna (bold circle) at 38 °C (Dewar & Graham 1994; Dewar *et al.* 1994) is provided for comparison.

The energetic costs of endothermic fish also support these findings. Countercurrent heat exchangers allow many species of tuna to conserve metabolic heat and achieve periods of endothermy (Dewar & Graham 1994). Consequences of this thermal specialization (and associated physiological and biochemical modifications) are higher maintenance and transport costs in comparison with ectothermic species. Thus, the $\mathrm{COT_{TOT}}$ for yellowfin tuna (*Thunnus albacares*, mean fork length = 51 cm) swimming at 25 °C is 2.75 $\mathrm{J\,kg^{-1}\,m^{-1}}$; a value that is 56% higher than predicted for salmonids swimming at the same temperature (Dewar & Graham 1994). By using a Q_{10} of 1.67 determined for yellowfin tuna (Dewar & Graham 1994), we can calculate the theoretical $\mathrm{COT_{TOT}}$ for tuna swimming at a mammalian temperature of 38 °C. The resulting value is within 7% of the predicted $\mathrm{COT_{TOT}}$ for a similarly sized marine mammal (see figure 2). Although it is unlikely that a tuna would experience such an increase in core temperature (Dewar *et al.* 1994), these calculations serve to illustrate the pathways for evolutionary convergence associated with endothermy and cost efficient locomotion in large aquatic animals. Both mammals and fish are capable of locomotor thermogenesis, but it appears that the ability to retain endogenous heat dictates the difference in transport costs between these groups.

(b) *Comparisons with other mammalian athletes*

The disparate physical demands for moving on land, through water or through air result in perceptible differences in effort. Among elite animal athletes, evolution and training promote specialized body morphologies and locomotor mechanisms for each form of locomotion. Energetic transport costs usually reflect these specializations and the underlying physical demands of swimming, running and flying (Schmidt-Nielsen 1972; figure 3*a*). An interesting finding in the present study is the nearly identical allometric regressions describing $\mathrm{COT_{TOT}}$ for swimming in marine mammals and for running in terrestrial mammals (figure 3*b*). Rather than mode of locomotion, phylogenetic history appears to be an important factor in setting the total energetic cost of active mammals. Total cost of transport for running, swimming and even flying mammals can be described by a single allometric relation

$$\mathrm{COT_{TOT}} = 10.02\,\mathrm{mass}^{-0.31}\,(r^2 = 0.92),$$

where $\mathrm{COT_{TOT}}$ is cost of transport in $\mathrm{J\,kg^{-1}\,m^{-1}}$ and body mass is in kilograms ($n = 55$ individual values representing four species of bat, and 29 terrestrial and six marine mammal species). This relation is indistinguishable from regressions describing transport costs for mammals specialized for running or swimming; bats, however, show $\mathrm{COT_{TOT}}$ for flying that are slightly lower than predicted by this regression (figure 3*b*). Neither the slopes nor y-intercepts of the allometric regressions for obligate terrestrial or marine mammals are significantly different from the combined regression (table 2). An important factor in these energetic relations is specialization for one mode of locomotion. The allometric regression for semi-aquatic mammals is significantly different from that describing $\mathrm{COT_{TOT}}$ for terrestrial mammals (y-intercept $t_5 = 4.874$, $p < 0.005$; slope $t_5 = 3.113$, $p < 0.05$). In contrast, comparisons between the regressions for marine and terrestrial mammals demonstrate no significant differences for these locomotor specialists (y-intercept $t_8 = 0.558$, $p > 0.25$; slope $t_8 = 0.172$, $p > 0.25$). Thus, we find that the cost of running in a 28 kg goat is identical to the cost of swimming in a 32 kg harbour seal. A 24 kg running dog incurs costs that are only 6% higher. A 107 kg horse maintains a cost of transport within 25% of the cost of swimming for a 104 kg grey seal. $\mathrm{COT_{TOT}}$ for a swimming bottlenose dolphin approaches that of a running eland. By comparison, similarly sized semi-aquatic mammals incur costs that are 3–4 times higher.

It is important to recognize that the relative energetic contribution of locomotor and maintenance processes to $\mathrm{COT_{TOT}}$ differs for mammals specializing in swimming, flying or running. In general, a greater proportion of the $\mathrm{COT_{TOT}}$ is comprised of maintenance costs for many marine mammals in comparison with terrestrial or aerial mammals (figure 4). For example, 22–77% of $\mathrm{COT_{TOT}}$ was comprised of maintenance costs in pinnipeds, sea otters, and bottlenose dolphins (table 1). This compares with only 12% in terrestrial mammals and 14% in bats.

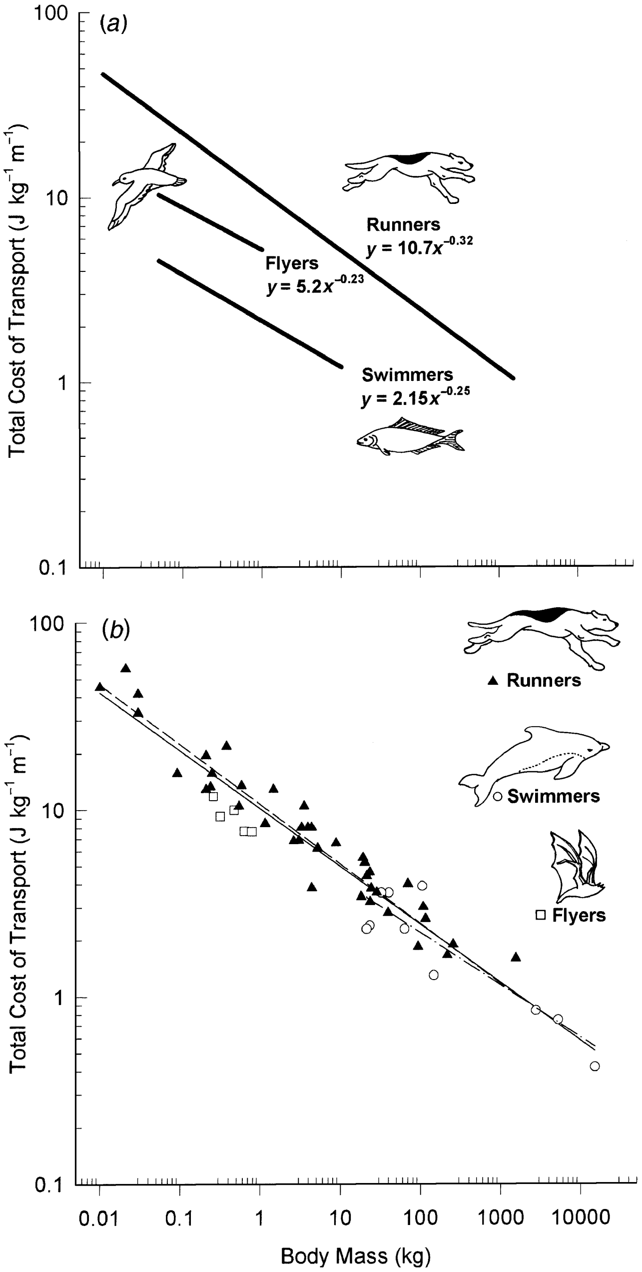

Figure 3. Total cost of transport in relation to body mass for different classes of vertebrates. The conventional comparison for swimming fish, running mammals and flying birds (*a*) is compared with swimming (open circles), flying (open squares) and running (filled triangles) mammals (*b*). (*a*) Regressions are from Tucker (1973) for flyers, Taylor *et al.* (1982) for runners, and Brett (1964) for swimmers, and is based on Schmidt-Nielsen (1972). (*b*) The solid line represents the $\mathrm{COT_{TOT}}$ regression for all mammals including flying bats ($n = 5$), swimming marine mammals ($n = 10$) and running terrestrial mammals ($n = 40$). Individual values in (*b*) are from Taylor *et al.* (1982) and Langman *et al.* (1995) for terrestrial mammals, Carpenter (1985, 1986) for bats and as in figure 1 for marine mammals. The dashed and stippled lines show allometric regressions for running and swimming mammals, respectively.

These results support the theoretical predictions of Peters (1983) who suggested that the higher total transport costs of swimming homeotherms in comparison with swimming poikilotherms was owing primarily to proportionately higher maintenance metabolic costs.

Table 2. T-*test statistics comparing the allometric regression describing transport costs for locomoting mammals*

(Costs for all locomoting mammals ($\mathrm{COT_{TOT}} = 10.02\ \mathrm{mass}^{-0.31}$, $n = 55$, $r^2 = 0.92$) are compared to the regressions for swimming marine mammals ($\mathrm{COT_{TOT}} = 7.79\ \mathrm{mass}^{-0.29}$, $r^2 = 0.83$, $n = 10$) and running terrestrial mammals ($\mathrm{COT_{TOT}} = 10.7\ \mathrm{mass}^{-0.32}$ from Taylor *et al.* 1982). Regressions for cost of transport versus body mass (log–log transformed) were determined using least squares methods (Zar 1974). Differences in the slopes and *y*-intercepts of allometric regressions for marine and terrestrial mammals, and for semi-aquatic mammals and locomotor specialists were evaluated. Regression parameters were computed from the sources and data in table 1 for marine and semi-aquatic mammals, and taken from the published literature for running mammals (Taylor *et al.* 1982) including elephants (Langman *et al.* 1995).)

	y-intercept	slope
terrestrial mammals		
t_{38}	1.6	0.5
$p>$	0.05	0.25
marine mammals		
t_8	0.42	0.13
$p>$	0.25	0.25

When LC and MC are taken into account, the results of this study remain consistent with previous studies concerning the relative energetic cost of swimming, flying and running (Schmidt-Nielsen 1972; Tucker 1975). That is, the cost of swimming is lower than that of other forms of locomotion (figure 3*a*). In mammals specialized only for swimming, LC rather than $\mathrm{COT_{TOT}}$ resemble the values predicted for fish (figure 2). The implication is that the energy dedicated to moving the body and limbs varies with locomotor mode and is most economical for swimmers. However, the total energetic cost ($\mathrm{COT_{TOT}}$) incurred by the swimming marine mammal is much higher. It is this total cost that cannot be distinguished from values reported for mammalian runners and flyers (figure 3*b*). Viewed as the entire energetic demand required for moving from one place to another, $\mathrm{COT_{TOT}}$ takes on an ecological relevance. Free-ranging animals must contend with the total energetic expenditure associated with supporting basic biological functions as well as with moving the body and appendages through the environment. $\mathrm{COT_{TOT}}$ provides an indication of the sum of these expenses, and perhaps should be termed the excursion cost or ecological cost of transport (Garland 1983) to differentiate it from the standard usage of cost of transport.

(c) *Optimizing oxygen delivery during locomotion*

It is not intuitively obvious why the cost of swimming in fish should be lower than flight in birds and why both of these are energetically cheaper than running. Indeed, the high drag of the aquatic environment would have suggested the opposite. Runners must expend energy to overcome gravity, whereas swimmers overcome hydrodynamic drag, and flyers contend with both aerodynamic drag and gravity (Schmidt-Nielsen 1972). To date, it is unclear which of these, if any, posed the greatest evolutionary challenge to mammalian energetic pathways.

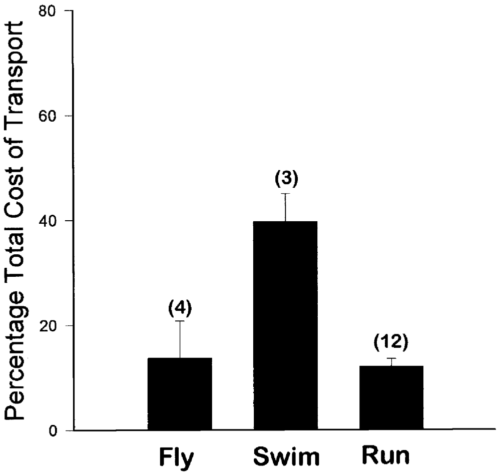

Figure 4. Percentage of $\mathrm{COT_{TOT}}$ attributed to maintenance costs in flying, swimming and running mammals. Height of the bars and vertical lines represent mean percentage of $\mathrm{COT_{TOT}} + 1$ s.e. for each group. Maintenance costs were determined from the metabolic rates of animals resting in air or water prior to exercise as described in the text. Data are from sources cited in figure 3. Numbers in parentheses represent number of species.

The similarity in total transport costs for terrestrial, aquatic and aerial mammalian specialists (figure 3*b*) suggests a physiological rather than mechanical limit for $\mathrm{COT_{TOT}}$. Tucker (1975) indicated that the comparatively low mean muscular efficiency of running animals accounted for their higher costs of transport. Similarly, Taylor and colleagues (Taylor *et al.* 1980; Taylor 1987) have proposed that the observed differences in transport costs between swimmers, runners and flyers may result from differences in the cost of generating muscular force rather than in doing work against the environment *per se*. Variations in the energetic cost for size-specific recruitment of individual fibre types in skeletal muscles may also account for differences in transport costs (Rome 1992).

A closer examination of the two parameters used to calculate transport costs, locomotor velocity and the rate of oxygen consumption during exercise, provides additional insights regarding the costs for different modes of locomotion. The velocities associated with the minimum $\mathrm{COT_{TOT}}$ for different forms of locomotion do not follow the pattern observed for running, swimming and flying costs. Swimming fish and running mammals of comparable body mass tend to move at similar minimum $\mathrm{COT_{TOT}}$ speeds, whereas flying birds move considerably faster (Peters 1983). For example, fish ranging from 0.06 kg salmonids (Brett 1964) to 2.2 kg yellowfin tuna (Dewar & Graham 1994) swim at $0.30–1.1\ \mathrm{m\,s^{-1}}$. Similarly sized mammals show minimum cost running speeds ranging from *ca.* $0.2\ \mathrm{m\,s^{-1}}$ to $0.6\ \mathrm{m\,s^{-1}}$ while similarly sized birds fly 15–30 times faster (Tucker 1973). Likewise, flying mammals move at $7–8\ \mathrm{m\,s^{-1}}$ while terrestrial counterparts barely approach $0.6\ \mathrm{m\,s^{-1}}$. The minimum $\mathrm{COT_{TOT}}$ speed is *ca.* $2.0\ \mathrm{m\,s^{-1}}$ for many marine mammals regardless of the size of the swimmer (Videler & Nolet 1990; table 1). Yet, a sea otter-sized terrestrial mammal runs at $0.8\ \mathrm{m\,s^{-1}}$ and a dolphin-sized terrestrial mammal shows a minimum $\mathrm{COT_{TOT}}$ speed of over $6.5\ \mathrm{m\,s^{-1}}$ (Taylor *et al.* 1982). Based on the relative costs for swimming, flying and running (figure 3*a*), the order in which we would expect the fastest performances would be: fish, birds, and terrestrial mammals. Instead, flyers routinely outperform both runners and swimmers.

The ability of an animal to take in, deliver and translate oxygen into muscular work during exercise affords a qualitative explanation for the differences in COT_{TOT} for animals. Structural and functional variations along the respiratory system appear to correlate with limits in oxidative metabolism (Weibel *et al.* 1987; Taylor *et al.* 1987*a*). The diffusing capacity of the lungs, cardiac output, and capillary volume and total mitochondrial volume within the locomotor muscles are important factors in setting the aerobic capacity of terrestrial athletes (Taylor *et al.* 1987*b*). Comparable details are not available for the respiratory pathways of other vertebrate groups. However, comparisons of the efficiency of gas-exchange organs have been made for piscine, avian and mammalian systems. These studies indicate that the countercurrent gills of fish are the most efficient vertebrate respiratory system for extracting oxygen from the surrounding medium. This is followed by the cross-current system of birds and finally the open pool system of mammals (Piiper & Scheid 1982; Scheid 1982). Interestingly, the relative differences in COT_{TOT} for swimming fish, flying birds and running mammals (figure 3*a*) parallel the theoretical sequence in gas exchange efficiency among these vertebrate groups.

It is likely that the gas-exchange systems of these groups operate below their theoretical limits under normal physiological conditions (Scheid 1982). Yet, inherent differences in the efficiency of the oxygen pathway, whether at the level of the oxygen uptake, delivery or use by the skeletal muscles, could provide clues about the relation between physiological limits and the optimum energetic costs during locomotion. Mammals tend to preferentially select locomotor speeds that result in the lowest energetic cost (Hoyt & Taylor 1981). If the oxygen pathway operates at near maximum efficiency at these preferred speeds, then the similarity in COT_{TOT} for mammals regardless of whether they are swimming or running (figure 3*b*) is not as surprising.

Clearly, further research regarding the efficiency of the oxygen pathway for different mammalian groups is needed. In addition, it is difficult to predict if the same patterns will apply to other vertebrate groups. Evolutionary pressures as well as the malleability of the oxygen pathway may be very different for birds, lizards and fish, and warrant further investigation.

(d) *The evolution of cost efficient swimming in mammals*

These results permit us to speculate about the energetic challenges faced by ancestral marine mammals. The physiological building blocks available to the first mammalian expatriates into the aquatic environment would have been those of a terrestrial specialist, i.e. a mammal designed primarily for moving on land. Assuming that the same physiological constraints act on extant mammals, the energetic trend during evolution would have been from the low transport costs of the terrestrial specialist to the high costs of amphibious species followed by a return to the initial low cost level in the aquatic specialist (see figure 5). With increased morphological specialization (Fish 1996), and consequently increased proficiency in the water, energetic costs for locomotion could be reduced. Thus, in evolving an aquatic lifestyle primitive marine mammals probably encountered and overcame an energetic hurdle in terms of transport costs only to return to energetic levels dictated by their terrestrial ancestry. Such an energetic hurdle initially seems counter to the argument that natural selection maximizes fitness along an evolutionary pathway. However, locomotor and physiological mechanisms are only part of the energetic equation for ancestral animals (Alexander 1996). The selective forces for entering the aquatic environment (i.e. favourable climatic conditions, ecological or habitat opportunities, the exploitation of previously untapped food resources; Fordyce 1989; Fordyce & Barnes 1994) undoubtedly provided an energetic benefit to the mammal. Presumably, these benefits surmounted the energetic difficulties associated with entering the water. Furthermore, limiting the duration of initial forays into the water may have reduced energetic disadvantages in the form of high maintenance and locomotor costs. This strategy is observed in extant semi-aquatic mammals such as the North American mink (*Mustela vison*; Williams 1986) and Australian water rat (*Hydromys chryogaster*; Fanning & Dawson 1980). By maintaining a labile core body temperature and limiting aquatic activity to short periods these mammals gain the energetic advantage of additional prey resources while minimizing energetic disadvantages. Consequently, minks and water rats establish an overall balance in costs and benefits by shuttling between energetic peaks and valleys. A similar mechanism in ancestral marine mammals would have relegated the proposed energetic hurdle to a transient phenomenon.

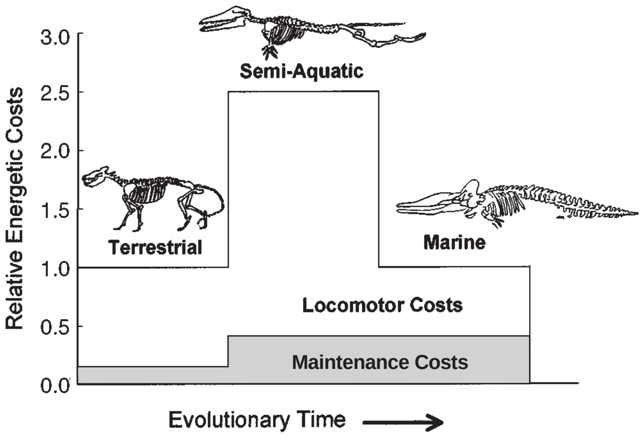

Figure 5. Theoretical changes in COT_{TOT}, locomotor costs and maintenance costs with the evolution of fully marine living mammals. The evolutionary pathway assumes that ancestral marine mammals included an obligate terrestrial form that was followed by a semi-aquatic form (i.e. *Ambulocetus*) and finally an obligate marine form. The solid lines at the top denote relative COT_{TOT}. The white and grey areas designate locomotor and maintenance costs, respectively. Note the similarity in COT_{TOT} for terrestrial and marine specialists despite the change in the relative contribution of locomotor and maintenance costs. (Skeletons redrawn from Berta 1994.)

The resulting $\mathrm{COT}_{\mathrm{TOT}}$ for extant marine mammals are higher than predicted for salmonid fish, but further evolutionary or energetic improvements are unlikely. Without the energetic burden of endothermy many marine mammals show locomotor costs approaching those of fish, a group that has the lowest cost of transport among vertebrates (Schmidt-Nielsen 1972). If, as these results imply, marine mammals have reached an energetic optimum in terms of locomotor costs, then $\mathrm{COT}_{\mathrm{TOT}}$ may only be reduced by altering the comparatively high maintenance costs (figure 4). This may be accomplished by entering a hypometabolic state, an energy conserving strategy observed for some marine mammals during prolonged apneas associated with diving (Hochachka & Guppy 1987; Hurley 1996). Such a physiological mechanism may also explain the exceptionally low transport costs of submerged-swimming beavers (Allers & Culik 1997) and platypus (Fish *et al.* 1997).

Current evidence suggests that specialists among mammals have converged on an energetic optimum for locomotion. Unexpectedly, the phocid seals, otariids, odontocetes and mysticetes independently evolved into forms with swimming transport costs equivalent to those of running mammals. Regardless of the style of propulsion or locomotor mode (figure 3*b*), mammals appear to expend similar levels of energy to move a kilometre, albeit at different speeds and maintenance costs. This implies a preferred limit in aerobic efficiency along the pathway for oxygen in mammalian systems. Taylor and colleagues (1987*a*,*b*) have suggested that structural and functional limitations along this pathway dictate aerobic performance capacities in terrestrial athletes. The present study indicates that similar limitations may apply to aquatic mammals. To maximize performance within these limitations the energetically efficient swimmer will specialize for one locomotor event, and thus improve chances for successfully hunting prey, escaping predators or winning in Olympic competitions.

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