The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks

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Summary. 1. Rates of oxygen consumption ($\dot{V}_{O_2}$) during surface and subsurface swimming were measured in the little penguin *Eudyptula minor*. Comparisons were made with a duck of similar body mass, *Anas superciliosa*.

2. For both species, swimming on the water surface showed a marked curvilinear increase in $\dot{V}_{O_2}$ with speed above 0.5 ms^{-1}. Swimming while completely submerged reduced the oxygen demands in penguins by about 40%.

3. In ducks and penguins, increase in swimming speed was associated with modulation of both limb frequency and stride length.

4. In total efficiency of surface swimming (the ratio of mechanical power output to metabolic power input), the value for the penguin was 4.5% and for the duck, 5.7%.

5. The mass specific oxygen demand to move a given distance decreased from walking to surface swimming to submerged swimming in the penguin. The value for the duck whilst swimming on the surface was greater than that for the penguin.

6. Sub-surface swimming in penguins shows energy demands lower than for any other swimming endotherm.

Introduction

Among the many avian species with aquatic habits, two groups can be recognised, those which use their legs for propulsion and those which use their wings. The ducks (Anatidae) and grebes (Podicipedidae) are examples of the first group, the petrels (Pelecanoididae) and penguins (Spheniscidae) represent the second (see Storer 1958). This division by pattern of limb usage is maintained whether swimming on the surface or when underwater.

Studies of the energy demands and biomechanics of animals moving in water have centred on fish. Recent reviews by Blight (1977) and Blake (1983) indicate the advanced state of understanding of many aspects of fish locomotion. Fewer studies have been undertaken on other vertebrates. The metabolic cost of swimming in reptiles has been measured in sea turtles (Prange 1976) and marine iguanas (Vleck et al. 1981) and in ducks by Prange and Schmidt-Nielsen (1970) and Woakes and Butler (1983). There have been several reported studies in mammals, the California sea lion (Costello and Whittow 1975; Kruse 1975), the muskrat (Fish 1982) and the mink (Williams 1983). Di Prampero et al. (1974) assessed the energetics of swimming in man. Two generalisations have emerged from these studies, firstly that surface swimming is energetically expensive compared to the energy expended by fish in moving under water, and secondly, that unlike terrestrial locomotion, surface swimming may show a curvilinear increase in the rate of energy usage with increasing speed.

The two bird species used in this study were the black duck and the little penguin. The black duck *Anas superciliosa* is found throughout Australia on fresh and brackish waters. It belongs to the group of closely related species allied to the mallards (Frith 1977). The little penguin *Eudyptula minor* nests around the southern coasts of Australia and it is the smallest member of the family Spheniscidae. In this paper we examine the energy expenditure for locomotion in both species: surface swimming in the duck, and walking, swimming on the surface and while completely submerged for the penguin.

Materials and methods

Animals Eight little penguins were obtained from Kangaroo Island, South Australia. They were kept in an outside enclosure and provided with artificial nesting burrows and a circular swimming tank (3 m diameter, 0.6 m deep) containing filtered fresh water. The concrete floor of the enclosure was covered with fine shell material and sand. The birds were hand-fed twice daily on a diet of brine-soaked small fish (150–200 g/day) supplemented weekly with a multi-vitamin formula. The experiments reported here were repeated over an 8 month period during which time the birds maintained body mass around 1.2 kg. Black ducks were supplied from a field population in Werribee, Victoria. They were housed outdoors and maintained on commercial food pellets and drinking water. The birds were maintained on a natural earth surface and had access to a small 2 m square swimming pool. Under these conditions, the four birds used in the study maintained body weight around 1.1 kg. All birds followed similar daily training regimes over a period of a month before steady performances were achieved each day. The penguins responded to training much better than the ducks. We were unable to train the latter species to walk in a steady manner on the treadmill, nor would they swim horizontally underwater, showing a clear preference for short dives. The penguins responded well to training and readily swam and walked in the apparatus.

Apparatus. Both species of birds were trained to swim in an annular water flume with a working section 0.6 m long, 0.6 m wide and 0.5 m deep. Water was circulated using a variable speed 2 kW electric motor attached to a vertical drive train and propeller. Turbulence was reduced by placing a screen of plastic tubes 20 mm in diameter and 220 mm long in front of the working section. In the region where the animals swam, water velocity was measured with an Ott current meter (Type F4) previously calibrated with Pitot tubes. We estimate that our measurement had a maximum systematic error of 5%. The degree of turbulence was assessed using the simple technique of Prange and Schmidt-Nielsen (1970). A dye stream was introduced in front of the working section at a depth of 0.05 m. At the rear of this section, the introduced dye had spread to an area of between 0.02 and 0.04 m in width over a range of speeds from 0.3 to 0.7 m·s^{-1}. Net water movement perpendicular to the flow stream was therefore less than 6%.

For studies of terrestrial locomotion a level motor-driven treadmill was used. The belt was driven through an hydraulic drive system which provided constant speed even at the lowest settings. The speed indicator of the system was calibrated from the length of the belt and the time for a counted sample of revolutions.

Determinations of rates of oxygen consumption ($\dot{V}_{O_2}$). For swimming experiments the animals were enclosed in a plexiglass chamber suspended just above the water surface, and a curtain of rubber sheeting formed an incomplete seal with the water surface. The anterior portion of the chamber was enlarged and formed the functional part of the respiratory chamber. Air was drawn from a port behind the bird's head at flow rates around 30 l min^{-1}. A slightly negative pressure was maintained in the chamber, but this never exceeded 2 mm Hg. The air coming from the chamber was pumped into a 3 l mixing chamber, dried and passed through a rotameter. A subsample was fed to one channel of a Servomex (Model OA184) oxygen analyser. An identical parallel circuit provided room air to the second channel of the instrument. The rate of oxygen consumption was determined from the equation (3a) of Withers (1977) and corrected to standard conditions of temperature and pressure of dry gas. Four birds of each species were trained to maintain position in the apparatus while swimming on the surface with their heads always above water. Most tests were of 20 min duration and stable ($\pm 5\%$) readings over at least 10 min were reported. Measurements of oxygen consumption were also taken from animals floating on still water. During this time the chamber was covered and the animal was in semidarkness. The experiments were conducted indoors during the normal daylight period of the birds. Ambient and water temperatures varied over the range 19–22.5 °C. The rate of energy usage ($\dot{E}_{metab}$) was calculated using an equivalent of 5.6 Watt per litre O_2 h^{-1}.

To collect expired respiratory gas from walking penguins the birds were fitted with light-weight masks fashioned from plastic centrifuge linings. From the mask, air was drawn at rates around 6 l min^{-1}. The mask and gas line was suspended from a framework above the animal and little extra load was incurred. The birds would readily walk for periods up to 6–8 min at the speeds used. The fractional concentration of oxygen in the gas stream and room air was measured in an identical manner to that in the swimming experiments.

Sub-surface swimming. The metabolism chamber was fitted with a trapdoor which could be operated from outside. Cut into this trapdoor was a second smaller door of dimensions approximating the width of the animal's head and neck. By careful manipulation of these doors, 3 of the penguins were induced to swim while completely submerged, but only at the higher water speeds. Most birds would surface about every one to two minutes of a swimming period, and even with a large mixing vessel in the gas line a constant level of oxygen usage could not be recorded. The trace from the experiments was therefore integrated using a digitising pad and associated software. The ducks could not adapt to the training procedure and no measurements of steady state $\dot{V}_{O_2}$ were obtained. All sub-surface activity in the birds was restricted to steep shallow dives, a pattern which we could not modify by training.

Calibration. The flowmeters were initially calibrated against a clinical spirometer. After each measurement of $\dot{V}_{O_2}$, nitrogen gas was metered into the metabolism chamber from a precision flowmeter at a rate which provided a similar response on the oxygen analyser as a swimming bird. From this dilution of room air by nitrogen, the rate of air flow leaving the chamber was checked. The measurements from the flowmeter on the chamber exhalent line and those calculated from the nitrogen dilution method were always within 3%, demonstrating that at flowrates of 30 l/min, there was no detectable loss of gas from the chamber. Measurements of $\dot{V}_{O_2}$ have a maximum propagated systematic error of 5%.

Measurement of limb frequencies. Limb frequencies in swimming animals were taken from filmed records through a window on the side of the working section of the flume. All measurements are from birds swimming on the surface of the water. Filming was conducted at 200 frames s^{-1} using a Milliken DBH-5 camera on birds swimming horizontally at constant speed. Mean frequencies are reported from samples involving at least 5 complete limb cycles. In experiments with penguins walking on the treadmill, step frequencies were counted by eye.

Drag measurements. One of the penguins died sometime after the completion of our experiments and its body was used to determine drag. It was frozen in a natural swimming position with the wings held horizontally. The carcass was attached to a force transducer (Grass Instruments), previously calibrated with known weights, and the drag forces measured at the same range of speeds used in earlier experiments. We were only able

to obtain measurements from the carcass floating on the surface. At high water speeds representative of under-water swimming, the body was unstable.

Results

Energy expenditure during swimming

While swimming on the surface, the mean values of $\dot{V}_{O_2}$ in penguins were independent of swimming speed up to 0.52 m s^{-1} (Fig. 1). The mean values at speeds of 0.62 and 0.72 ms^{-1} are significantly different (Student's t-test; $P<0.05$) from each other and greater than all other values. For black duck, mean values of oxygen consumption at the slowest speed of 0.29 ms^{-1} is significantly lower than at any other speed, but when swimming at between 0.35 and 0.52 ms^{-1}, $\dot{V}_{O_2}$ is independent of speed. At swimming speeds above 0.52 ms^{-1}, the abrupt increase in $\dot{V}_{O_2}$ was statistically significant and the mean values at the two highest speeds (0.62 and 0.72 m s^{-1}) are significantly greater than all other mean values. Analysis of variance shows that at any swimming speed, the metabolic cost for the duck exceeds that of the penguin ($P<0.05$).

The mean values of $\dot{V}_{O_2}$ from penguins resting on the water surface was $1.14\pm$(SE) 0.46 l O_2(kg h)$^{-1}$, (6.40$\pm$0.47 W kg^{-1}) and for ducks 1.10$\pm$0.147 l O_2 (kg h)$^{-1}$, (6.19$\pm$0.34 W kg^{-1}). The mean value of $\dot{V}_{O_2}$ at the maximum speeds

that we could use were 2.23 l O_2 (kg h)$^{-1}$ for penguins and 3.24 l O_2 (kg h)$^{-1}$ for ducks, suggesting that penguins were operating at metabolic levels about twice the resting level, ducks at about three times.

Energy expenditure during walking

The mass specific metabolic rate increases linearly with walking speed in little penguins (Fig. 1). The equation describing this relationship is:

$$y = 1.38 + 3.64\ x\ (r = 0.86)$$

where y is metabolic rate in l O_2 (kg h)$^{-1}$, x the speed of walking in m s^{-1}. The change in metabolic rate with walking speed, 1.03 ml O_2/m kg (the slope of this line from recalculated data) is similar to that reported for the white flippered penguin $E.$ $albosignata$ by Pinshow et al. (1977) and is about 60% greater than that predicted from the equation of Taylor et al. (1982).

Swimming beneath the water surface

Data from 20 successful experiments on 3 penguins are included in Fig. 1. The mean values at speeds of 0.62 and 0.72 ms^{-1}, 1.33$\pm$0.10 and 1.51$\pm$0.31 l O_2 (kg h)$^{-1}$, are significantly lower ($P<0.05$) than those from surface-swimming penguins, 1.97$\pm$0.05 and 2.23$\pm$0.07 l O_2 (kg h)$^{-1}$ respectively.
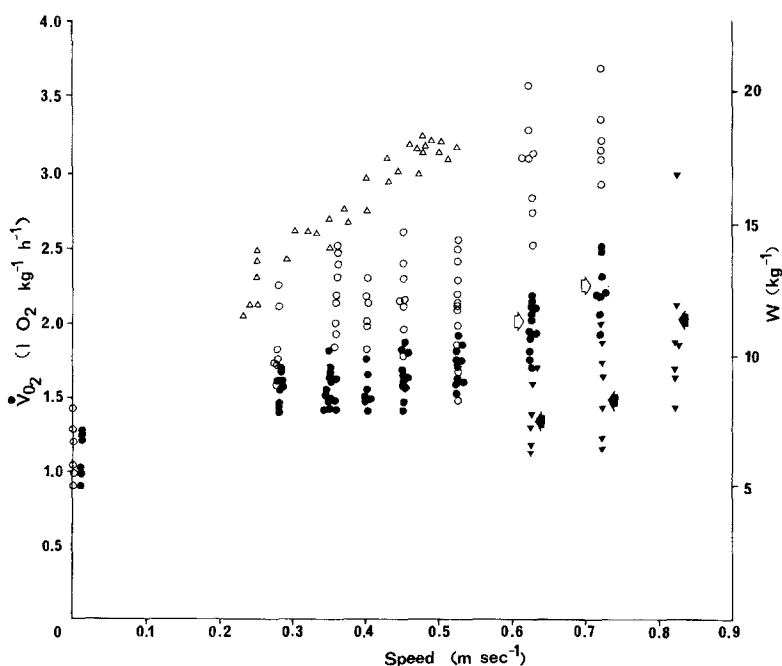
Fig. 1. Mass-specific oxygen consumption, $\dot{V}_{O_2}$, plotted as a function of speed for penguins and ducks. Closed arrows indicate mean values of $\dot{V}_{O_2}$ during sub-surface swimming, open arrows for surface swimming △ Running penguins; ○ swimming ducks; ● swimming penguins; ▼ sub-surface penguins
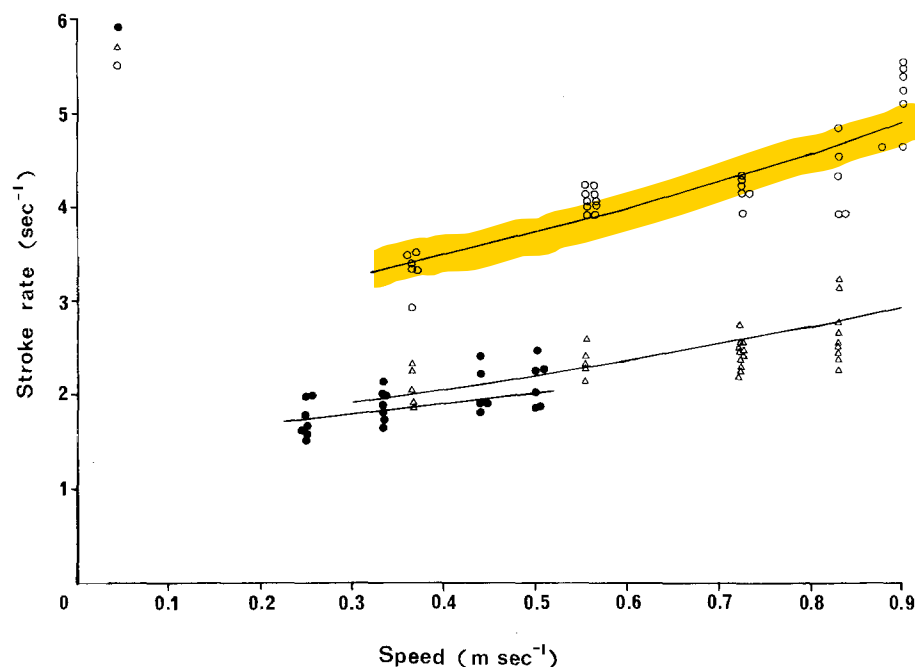
Fig. 2. Stroke frequency of flippers and legs during swimming and walking, respectively, in penguins, and stroke frequency of the legs in swimming ducks. ● running penguins; △ swimming ducks; ○ swimming penguins

Table 1. Efficiency of locomotor activity of penguins and ducks. Mechanical power output (P_o) was derived from the product of total body drag times the speed. The drag figures for the duck are those of Prange and Schmidt-Nielsen (1970). Oxygen consumption rates were converted to metabolic rates assuming that 1 ml of O_2 has a caloric equivalent of 20.1 J, hence 1 litre of O_2 consumed in 1 h is equivalent to 5.6 W

Swimming speed m s^{-1}	Metabolic power input, P_i (W)		Mean drag (Newtons)	Mechanical power output, P_o (W)	Efficiency P_o/P_i (%)	
	total	nett			total	nett
Penguins						
0.29	9.68	2.53 ± 0.016	0.120	0.0348	0.30	1.38
0.35	9.63	2.49 ± 0.11	0.165	0.0578	0.60	2.32
0.40	9.69	2.55 ± 0.010	0.196	0.0784	0.81	3.07
0.45	10.24	3.11 ± 0.12	0.242	0.109	1.06	3.50
0.52	10.75	3.61 ± 0.198	0.433	0.225	2.09	6.23
0.62	12.33	5.19 ± 0.032	0.601	0.373	3.02	7.19
0.72	13.96	6.82 ± 0.016	0.882	0.635	4.54	9.31
Ducks						
0.29	11.26	4.45	0.13	0.038	0.034	0.85
0.35	13.48	6.67	0.156	0.055	0.041	0.82
0.40	12.67	6.06	0.225	0.090	0.071	1.49
0.45	13.44	6.63	0.318	0.143	1.06	2.16
0.52	13.58	6.77	0.666	0.346	2.54	5.11
0.62	18.57	11.67	1.17	0.725	3.90	6.16
0.72	19.89	13.08	1.56	1.123	5.65	8.59

Limb frequency

As swimming speed increases, both penguins and ducks increase the stroking rate of the limb providing propulsion (Fig. 2). For the little penguin, the association between wingbeat frequency (y) and speed (x) is best described by the equation, $y = 2.3 + 2.2\, x^{0.46}$ $(r = 0.74)$. For ducks, the association between the paddling rate of the foot and speed is much weaker $(r = 0.46)$, but the data are again fitted best by a power function $(y = 1.4 + 1.6\, x^{0.68})$. An analysis of covariance demonstrates that the exponent of these relationships is statistically similar but the elevations are significantly different. Hence at any given speed, the penguin flipper has a greater frequency of beating than the foot of

the duck, but both increase at proportionally the same rate with increasing speed. The relation between the frequency of limb movement (y) and walking speed (x) in penguins shows a weak power function relationship, $y = 1.3 + 0.9 \ x^{0.23}$ $(r = 0.42)$. Neither the slope nor the intercept of this line differs from that describing the same parameters in swimming ducks.

Efficiency of locomotion activity in penguins

The relationship between the drag force on a frozen carcass (Table 1) and water speed is curvilinear, best described by a power function:

$$y = 1.77 \cdot x^{2.28} \quad (r = 0.95)$$

where y represents the net drag in newtons; x represents the water speed in $m \ s^{-1}$.

The mechanical power output (P_O) during swimming is given by the product of the total drag on the body (D) times the swimming speed (S), i.e. $P_O = D \cdot S$; these values are given in Table 1. The measurements of $\dot{V}_{O_2}$ or metabolic power input (P_i) and mechanical power output (P_O), then enable a measure of total or gross efficiency (P_O/P_i).

There are however two components of P_i, a 'resting' component derived from measurements of $\dot{V}_{O_2}$ in birds floating on the water surface and the power increments necessary for locomotion. Following the pattern of Williams (1983) we have calculated both the total efficiency $(P_O/\text{Total } P_i)$ and the net efficiency $(P_O/\text{incremental } P_i)$. Values of both parameters increase with swimming speed in the penguins.

Discussion

Penguins, being amongst the most aquatic in habit among birds, would perhaps be expected to show compromise between the different selection pressures of life on land and in the water. In the energetics of their swimming, such compromise is not immediately evident.

Previous studies on penguins provide a basic metabolic and mechanical background to locomotion in the group. Clark and Bemis (1979) examined the swimming patterns of seven species from filmed records taken in a large holding facility at the Detroit Zoo. Among their sample were records of *E. minor*. Their results confirmed earlier suggestions that both the pectoralis muscle and an hypertrophied supracoracoideus muscle generate thrust, thus providing propulsion over both halves of the stroke cycle. Mill and Baldwin (1983) examined

the metabolism and structure of both these muscles in *E. minor* and demonstrated a structural and metabolic similarity suggesting primarily aerobic function. They concluded that the birds did not rely extensively on short bursts of swimming nor were they deep divers.

In a larger penguin species, *Spheniscus humboldti*, Butler and Woakes (1984) found that rates of aerobic metabolism during diving were similar to those at rest. This contrasts with the higher cost of voluntary diving in tufted ducks (Woakes and Butler 1983), indicating differences in the work required to overcome greater buoyancy and the probably lower efficiency for underwater locomotion.

In changing speed, penguins appear to modulate both the frequency of wingbeat and the 'stride length', the distance travelled between equivalent wingbeat phases. This contrasts with avian flight where wing frequencies are generally believed to be oscillatory (see Clark and Bemis 1979, for discussion). Drag coefficients and the effects of the feathered surface on boundary layers have also been investigated, but only on larger penguin species, the gentoo *Pygoscelis papua* (Nachtigall and Bilo 1980) and the emperor penguin (Kooyman et al. 1971; Clark and Bemis 1979). These studies estimate remarkably low drag coefficients, lower than for example in fish, and suggest that the smooth feather patterns of penguins may buffer formation of turbulence at the body surface.

In summary, the little penguin is capable of generating thrust over both halves of a wingbeat cycle, the frequency of this cycle is not fixed, and the energy for locomotion comes primarily from aerobic metabolism. The hydrodynamic profiles of other penguins, if typical of the group, would suggest extremely low components of both frontal and surface drag.

Less comparable information is available on the duck. Prange and Schmidt-Nielsen (1970) studied swimming in mallard ducks and showed that speed increase was served solely by modulation in the length of the stride; the stroke rate remaining constant over a threefold increase in swimming speeds. These authors were unable to measure drag on their animals, but reported figures from a comparable model which was matched in its affect on wave formation. Estimated drag values showed a steep curvilinear increase with swimming speed and appeared asymptotic with the theoretical maximum speed of the duck 'hull'. In a more recent study, Woakes and Butler (1983) measured $\dot{V}_{O_2}$ and leg beat frequency in the tufted duck *Aythya fuligula*. Their results show a similar curvilinear

relation between the rate of oxygen consumption and speed, with changes in leg beat frequency serving speed increase. Mean levels of $\dot{V}_{O_2}$ in this species at maximal swimming speeds were about 3.5 times the resting levels.

From the results of the present study, it is apparent that the metabolic power dissipated in swimming ducks always exceeds that in swimming penguins at equivalent speeds, and that both values are less than those found in walking penguins. We did not measure the drag in the black ducks, but although the total drag on a frozen penguin carcass followed the same power-curve form as the duck model used in the Prange and Schmidt-Nielsen study, at equivalent speeds the drag force was always slightly less (Table 1).

A similarity between the penguins and black ducks was the reluctance to swim on the surface at speeds in excess of around 0.7 m s^{-1}, even though at this speed, levels of $\dot{V}_{O_2}$ were still less than three-times the resting level. This supports the finding of Prange and Schmidt-Nielsen that the theoretical maximum speed of a hull, (the speed where the wave length of the bow wave equals the length of the hull water-line) occurs at speeds where the increase in $\dot{V}_{O_2}$ is much less than the typical 10 fold increase at maximum locomotory speeds seen in terrestrial endotherms (see Taylor et al. 1982).

The penguin is able to extend this limit by swimming submerged and thus avoid the major component of drag associated with wave formation on the surface. It was interesting that penguins would only swim submerged for prolonged periods at high water speeds, and that during these periods gliding phases were invariably observed. Swimming under water in penguins results in a reduction of about 30% in the rate of oxygen consumption from that observed in surface swimming. We were unable to successfully estimate the total drag forces on the carcass at the high flow rates consistent with submerged swimming. The body was markedly unstable, suggesting that the constant adjustments of flippers and feet seen in live birds during swimming lends stability.

Individuals of both species in this study modulated limb frequency with increasing speed, but the wingbeat frequency of the penguin was about double the stroke rate of the duck. Since the increase in rate with speed is similar in both, the relative contribution of stride length must also be similar in both birds. Prange and Schmidt-Nielsen (1970) found no change of stroke rate in mallard ducks at various swimming speeds, and suggested that the elastic components of the leg may aid this oscil-

latory pattern. In a recent study of swimming in North American mink, Williams (1983) also reports a forepaw stroke frequency that was constant over a wide range of swimming speeds. Damped mechanical oscillations tuned to some resonant frequency could minimise the energy required for the acceleration and deceleration of a limb, however an alternative explanation for the fixed limb frequencies seen in many moving animals is the optimal rate of muscle shortening for both maximum power output and mechanochemical efficiency (see Goldspink 1977). This means that any significant change in frequency attracts a penalty in efficiency of muscle activity. The relation of this theoretical suggestion to the different patterns seen in swimming animals remains to be resolved.

To estimate the gross efficiency of swimming in penguins and ducks, we have used the ratio of the work done on the external environment to the metabolic rate. The latter term has a maintenance or 'resting' component and an incremental component associated with locomotion; in order to derive a measure of net efficiency the mean value of $\dot{V}_{O_2}$ in resting birds was subtracted. Like Prange and Schmidt-Nielsen (1970) we prefer comparisons of total efficiency due to uncertainty of baseline subtractions of the resting level (see Stainsby et al. 1980). At all swimming speeds, the data show a slightly greater efficiency for penguins than ducks. However with the inherent uncertainty in the estimates of drag forces derived from models or carcasses, we view this difference as insignificant. Both species approach 5% overall efficiency at their maximum surface speeds, a value similar to that in mallard ducks (Prange and Schmidt-Nielsen 1970).

Williams (1983) has performed similar measurements to these on swimming North American mink *Mustela vison*. The reported values of total locomotory efficiency showed a similar pattern of increase with swimming speed to the birds in this study, but values which were significantly lower. For example, at a similar maximum speed of 0.7 m s^{-1} mink have a value for total efficiency of 1.43% compared with the little penguin of 5.65 and the black duck of 4.54%. While the estimates for the total drag forces in all 3 species are similar, a marked difference is evident in the metabolic power input at the maximum speed. Penguins and ducks dissipate around 14 and 20 watt respectively, whereas mink have metabolic rates in excess of 30 watt. Williams reports that the highest levels of $\dot{V}_{O_2}$ recorded from swimming mink were within 3% of $\dot{V}_{O_2 \text{ max}}$ for the males and 14% for females. Comparing these values for penguins, maximum
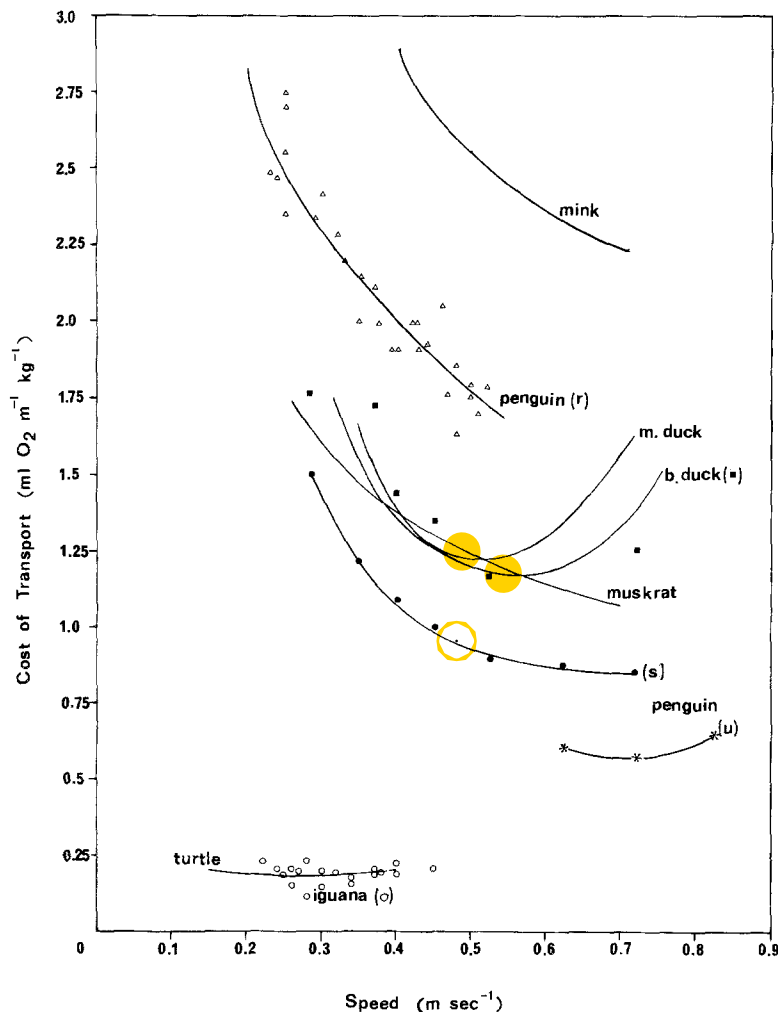
Fig. 3. The cost of transport as a function of speed in a variety of swimming vertebrates. Data for the iguana is from Vleck et al. (1981); for the turtle, Prange (1976); the muskrat, Fish (1982); mallard duck (*m. duck*), Prange and Schmidt-Nielsen (1970) and mink, Williams (1983). *b. duck* black duck. *r* running; *s* surface swimming; *u* sub-surface swimming

levels during swimming are only 70% of those found at the highest running speeds used.

There is comparable data from another aquatic mammal, the muskrat *Ondatra zibethicus* (Fish 1982). In this animal the maximum observed aerobic metabolism while swimming is less than four times the predicted resting level. Let us assume that muskrats, like most other mammals, are capable of maximal $\dot{V}_{O_2}$ levels around ten times resting metabolism. If this is the case, then muskrats, like ducks and penguins reach their maximum sustainable swimming speeds at metabolic levels considerably lower than the expected maximum. This contrasts with the mink where at high swimming speed levels of $\dot{V}_{O_2}$ are nearer maximal values.

In comparing different modes of locomotion, the ratio of mass specific metabolic rate to the velocity has been commonly used. This parameter, sometimes called the 'cost of transport' (see Tucker 1970; Schmidt-Nielsen 1972) expresses the effectiveness of transporting a unit of body mass

a unit distance. Values calculated from penguins and black duck and from the literature are plotted in Fig. 3. Among mammals and birds which spend time both on land and in the water, there is about a three-fold difference in the specific energy requirements to move a given distance. Many factors contribute to this difference, Williams (1983) comments on the paws of mink as inefficient thrust generators, whereas for example penguins may have near-optimal profiles for drag reduction. It is interesting when comparing these two animals at the extremes of locomotor costs, that the mink forages on both aquatic and terrestrial environments, but penguins gain all their food from the sea.

Finally, is there evidence of compromise in penguin energetics associated with aquatic and terrestrial locomotion? In common with Pinshow et al. (1977) we find that the minimal mass specific energy usage associated with walking is at the upper range of locomotory costs for birds and mammals.

Little penguins consume 1.01 O_2 $(kg \cdot km)^{-1}$ in walking, comparable with an equivalent value of 1.11 in *E. albosignata*, but considerably greater than the predicted value for birds (Taylor et al. 1982). Pinshow et al. have commented on the 'awkwardness' of the penguin gait and the large lateral displacement of the body. We were unable to induce our black ducks to walk on the treadmill, but they too have an 'awkward' gait and may be expected to show similar high relative energy costs.

In the water, penguins move with lower locomotory costs than other endotherms for which data are available. When swimming underwater, a further reduction is apparent, probably due to less drag-associated surface waves and an intermittent pattern of flapping. In selection for locomotory efficiency, penguins are specialised for water and therefore probably have compromised locomotion on land.

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