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ORIGINAL PAPER

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Energetics of foraging and locomotion in the platypus *Ornithorhynchus anatinus*

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Abstract We measured the energy requirements of platypuses foraging, diving and resting in a swim tank using flow-through respirometry. Also, walking metabolic rates were obtained from platypuses walking on a conventional treadmill. Energy requirements while foraging were found to depend on water temperature, body weight and dive duration and averaged 8.48 W kg^{-1}. Rates for subsurface swimming averaged 6.71 W kg^{-1}. Minimal cost of transport for subsurface swimming platypuses was 1.85 J $N^{-1}m^{-1}$ at a speed of 0.4 m s^{-1}. Aerobic dive limit of the platypus amounted to 59 s. Metabolic rate of platypuses resting on the water surface was minimal with 3.91 W kg^{-1} while minimal RMR on land was 2.08 W kg^{-1}. The metabolic rate for walking was 8.80 W kg^{-1} and 10.56 W kg^{-1} at speeds of 0.2 m s^{-1} and 0.3 m s^{-1}, respectively. A formula was derived, which allows prediction of power requirements of platypuses in the wild from measurements of body weight, dive duration and water temperature. Platypuses were found to expend energy at only half the rate of semiaquatic eutherians of comparable body sizes during both walking and diving. However, costs of transport at optimal speed were in line with findings for eutherians. These patterns suggest that underwater locomotion of semiaquatic mammals have converged on very similar efficiencies despite differences in phylogeny and locomotor mode.

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Abbreviations *ADL* aerobic dive limit · *COT* cost of transport · *LC* locomotor costs · *MC* maintenance costs

Introduction

The platypus *Ornithorhynchus anatinus* is the only prototherian mammal living today that has adopted a semiaquatic lifestyle. Its intermediate position between terrestrial and aquatic specialists suggests higher energy requirements for locomotion than specialised divers and walkers (Fish and Baudinette 1999) and these may be further increased by thermoregulatory constraints due to its relatively low body weight (Hind and Gurney 1997). However, the platypus is well established in a wide range of environments including Australia's alpine tableland areas where, in winter, it may be exposed to air temperatures well below freezing and water temperatures approaching 0 °C. This makes it evident that the species has the capacity to cope with severe environmental stresses despite its possible energetic constraints.

Platypuses can spend long periods continuously foraging in water at nearly 0 °C. Compared to other aquatic endotherms of similar size, anatomical and behavioural specialisation of the platypus makes it extremely well adapted to minimise loss of metabolic heat under these conditions (Grant and Dawson 1978a; Dawson and Fanning 1981). Also, resting metabolic rates of monotremes are reportedly lower compared to those of most eutherian mammals (Grant and Dawson 1978a; Dawson and Hulbert 1970). It is tempting to speculate that, just as the platypus has a lower resting metabolism and is better adapted to life in cold water than other semiaquatic mammals, it will also have very low energetic costs for swimming.

The efficiency of the swimming mechanism and the adaptations to the aquatic environment of the platypus have been disputed in the past (e.g. Howell 1937). Like other semiaquatic mammals, the platypus has a body form that deviates considerably from the optimal design to minimise drag (Fish 1992). Also, semiaquatic animals (which use paddling modes) in general have higher energy costs for swimming than specialised divers as determined from measurement of oxygen consumption (Fish 1982; Williams 1983a, 1989; Baudinette and Gill 1985; Fish 2000). However, Fish et al. (1997) suggested that the specialised rowing mode of the platypus in conjunction with enlarged and flexible forefeet for high thrust generation result in very efficient swimming.

In contrast, little is known of the energetics of walking in semiaquatic mammals, and it is in question as to whether their terrestrial locomotion follows the same energetic and mechanical patterns as that of specialised walkers (Fish and Baudinette 1999). Studies on the Australian water rat *Hydromys chrysogaster* (Fish and Baudinette 1999) and on the mink *Mustela vison* (Williams 1983b) found elevated costs of walking compared to similar sized terrestrial mammals. In consistence with results for specialised walkers (e.g. Taylor et al. 1970; Schmidt-Nielsen 1972; Taylor et al. 1982), the power requirements for walking increased linearly with increasing speed. The same was found to be true for the platypus (Fish et al. 2001). However, transport costs for walking in the platypus were reported to be lower than transport costs of specialised walkers (Fish et al. 2001).

The purpose of this study was to clarify the degree to which platypuses are specialised to the aquatic and terrestrial environment. The energetic costs of walking in the platypus were investigated on a conventional treadmill. A swim tank in conjunction with respirometry was used to determine energy consumption of the platypus while foraging and resting. A comparison with semiaquatic eutherians should provide further information on the energetics of the monotremes, and thus on the evolution of endothermy in mammals.

Materials and methods

A total of twelve platypuses, *O. anatinus* Shaw, from southern Tasmania were studied in a swim tank between July 1997 and September 1998 under permit from the Department of Parks, Wildlife and Heritage, Tasmania, the Inland Fisheries Commission, Tasmania and the University of Tasmania Ethics Committee. The animals (six females, mean body weight 1.20 kg, SD = 0.09; six males, mean body weight 1.84 kg, SD = 0.17) were caught in the Plenty River and associated tributaries at Salmon Ponds, Tasmania, following the methods outlined in Grant and Carrick (1974). Fyke nets were used in small creeks while unweighted gill nets were set in larger water bodies. All nets were checked at least every 20 min. Capture times ranged from 6 p.m. in the evening through to 4 a.m. in the morning. Catch per net hour averaged 0.07 for fyke nets and 0.23 for unweighted gill nets. Platypuses were held in captivity at the University of Tasmania animal house for 7–11 days each in a specially constructed platypussary based on the design of Manger and Pettigrew (1995). The animals were fed live mealworms, red compost worms and tigerworms and ate on average 170 g of food per night (SD = 56.1, *n* = 72 days). We observed an initial drop in body weight of 5% in the 1st 2 days after capture. Body weight stabilised or increased after day 3 of captivity.

The platypussary consisted of a fibreglass tank (1.4 m high, 2 m in diameter, water depth 90 cm) connected to a swim canal (3 m long, water depth 50 cm) and an artificial burrow. Water temperatures ranged between 8 °C in winter and 21 °C in summer. The water was constantly renewed and circulated by a swimming pool pump (Onga 600 Series) through a sand filter (Onga Pantera) at a rate of 275 $l\ min^{-1}$ while the tank level was adjusted by an overflow. Transparent plastic sheeting just beneath the surface of the water in the tank and swim canal prevented the platypuses from surfacing over most of the tank and canal surface. The animals were only able to surface and breathe in three respiration chambers, one at each end of the canal (volume 18.7 l) and one at the entrance to the burrow (volume 100 l). The chambers were constructed from transparent plastic, equipped with a mixing fan and were open to outside air. A wooden bank placed in the chamber at the burrow entrance, just above water level, allowed the platypuses to sit out of the water and groom. The artificial burrow consisted of a 13-m wooden tunnel (200×300 mm) approximating the natural burrow length of wild platypuses (Burrell 1927; Manger and Pettigrew 1995). Two nesting boxes (300 mm high×400 mm wide and long) were built in as part of the tunnel and dried sea grass was provided as nesting material. To enter the tank from the artificial burrow the animals had to pass a rubber tube (Ø 15 cm).

For the swim tank experiments, only one of the three chambers was connected to the system for better accuracy of the measurement. Air was drawn through the chamber by a pump at a mean flow rate of 20 $l\ min^{-1}$, measured by a mass flow meter (TYLAN model FM-380). A subsample of the air was dried and passed onto an oxygen-analyser (Applied Electrochemistry, Sunnyvale, Calif., model S-3A). Data from the oxygen-analyser and the mass flow meter were sampled every 0.5 s using a Mac Lab (Analog Digital Instruments, Castle Hill, NSW) and an Apple Macintosh Classic II Computer. The whole system was calibrated following Fedak et al. (1981) using known volumes of nitrogen. Mean measurement error was $<1\%$. The system was checked for leaks before each experiment.

Platypuses placed in the platypussary learned within two nights where they could surface to breathe and how to get from the swim tank into the artificial burrow and vice versa. Experiments started on day 3 after capture. Burrow access was closed after the animals had entered the swim tank at dawn and reopened after the experiments. Measurements were taken for an average of 6 h. During the experiments, the platypuses were continuously observed by a video camera mounted over the swim tank connected to a VCR. Activity and dive duration of the animals were later derived from the videotapes. To determine the effect of externally attached devices on the energy requirements of the platypuses, six animals were equipped with data loggers (weight 40 g) in about one third of the experiments.

Metabolic rates for walking were obtained from platypuses walking on a conventional treadmill in conjunction with respirometry. An additional respiration chamber (volume 28.3 l), constructed from transparent plastic sheeting, was placed on the treadmill for the experiments. The chamber was equipped with small wheels so that it could be fixed in a stable position on the treadmill. Data was only taken from animals walking constantly for at least 10 min.

Resting rates in water were measured during naturally occurring resting periods of the animals in the swim tank. Only data from resting periods longer than 5 min were used for analysis. Oxygen consumption while resting on land was measured using the open-circuit system and the additional respiration chamber (volume 28.3 l) described above. The chamber had to be covered with hessian bags during the experiments since the animals did not settle otherwise. Data was taken only from fasted animals resting quietly for at least 20 min.

To calculate the O_2-consumption a modification of the formula given by Woakes and Butler (1983) was used, which incorporates chamber volume and allows accurate measurement of fast changes in O_2-concentrations irrespective of the lag time of the system. Following Withers (1977), we corrected for the respiratory quotient of the platypus (RQ = 0.8; Brody 1945; Grant and Dawson 1978a;

Fish et al. 1997). To calculate the rate of oxygen consumption while foraging we assumed that O_2-consumption in the chamber was identical to the platypus's resting values at the water surface and subtracted the resting metabolism in the chamber from the total amount of oxygen consumed during the recovery period after each dive. (Culik and Wilson 1991; Bethge et al. 1997). Conversion into watts per kilogram was made assuming a conversion factor of 20.11 kJ l^{-1} oxygen (Grant and Dawson 1978a).

Individual platypuses were tested many times in the swim tank as well as on the treadmill. To account for repeated measures, mixed multiple regressions were calculated where random effects represented differences between individuals. Statistical tests were also made using analysis of variance (ANOVA) with individual ($n = 12$) as a random factor and the effects in question as covariates. Statistical testing was performed using SYSTAT.

Results

Resting metabolic rate in water and on land

The mean resting metabolic rate obtained from ten platypuses in air was 2.54 W kg^{-1} ($SD = 0.38$, $n = 10$, equals 0.46 ml O2 g^{-1} h^{-1}) and ranged between 2.08 W kg^{-1} (at 26 °C ambient temperature) and 3.26 W kg^{-1} (at 10 °C). Resting metabolic rates were significantly dependent on air temperature ($P < 0.001$) but not on the weight of the platypuses ($P = 0.052$). Lower air temperatures caused higher resting rates. Similarly, heat production in water increased gradually as water temperature decreased. The mean metabolic rate obtained from ten platypuses resting on the water surface was 4.81 W kg^{-1} ($SD = 0.91$, $n = 10$, equals 0.86 ml O2 g^{-1} h^{-1}) and ranged between 3.91 W kg^{-1} (at 21 °C water temperature) and 6.39 W kg^{-1} (at 9 °C). Resting metabolic rates in water were significantly dependent on water temperature ($P < 0.001$), but not on animal weight ($P = 0.725$). Platypus resting metabolic rates in air respectively water are best predicted by

$$P_{(\mathrm{REST})[\mathrm{in\ air}]} = 0.035\ T_{\mathrm{a/w}} + 24.49\ T_{\mathrm{a/w}}^{-1} + 0.3 (n = 14, r = 0.86) \quad (1)$$

and

$$P_{(\mathrm{REST})[\mathrm{in\ water}]} = 0.107\ T_w + 61.77\ T_{a/w}^{-1} - 1.48 (n = 47, r = 0.81) \quad (2)$$

where $T_{a/w}$ = air/water temperature (°C) and $P_{(REST)}$ is in W kg^{-1} (Fig. 1).

In the wild, platypuses wedge themselves occasionally under rocks and logs under the water surface, supposedly to hide in case of danger or emergency (Grant 1995). Occasionally, animals performed such 'wedging' behaviour in the swim tank underneath the plastic sheeting. On some occasions 'wedging' occurred close to one respiration chamber so that the platypus was able to stick its bill up above the water line to occasionally take a breath (a behaviour we have also observed in the wild under ice). Measurements for 'wedging' were obtained from those events in four animals. The mean metabolic rate for 'wedging' underwater was 3.46 W kg^{-1} ($SD = 0.46$, $n = 4$, equals 0.62 ml O2 g^{-1} h^{-1}) and varied with water temperature. Results for the resting metabolic rates of the platypus are summarised in Fig. 1.

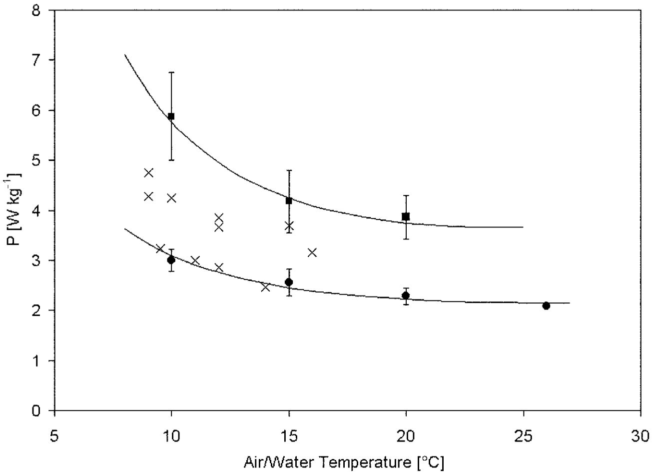

Fig. 1 Platypus resting metabolic rates in air and water, plotted as a function of air and water temperature respectively. Means ± SD shown for air and water. *Circles* = air, *squares* = water, *crosses* = wedging. *Lines* show predicted values

Metabolic rate and cost of transport for foraging and subsurface swimming

Foraging of platypuses in the swim tank could be divided into three phases. After diving to the bottom with obvious effort and fast movement of the propelling forelegs (phase-1), the animals foraged along the tank bottom moving their bill from one side to the other in a characteristic sweeping movement while searching for food (phase-2; for comparison, see Manger and Pettigrew 1995; Fish et al. 1997). They finally surfaced by simply stopping their movement and returning to the surface through the positive buoyancy of their bodies (phase-3). A total of 555 dives from 12 different platypuses were analysed. Active dives were between 5 s and 77 s in duration, averaging 23.5 s ($SD = 9.9$, $n = 12$). Only foraging bouts where all three phases were completed were used for analysis. To account for repeated measures, a mixed multiple regression was calculated (fixed effect: body mass, random effects: dive duration and water temperature). Foraging metabolic rate was significantly dependent on dive duration (within subjects: $P = 0.030$, between subjects: $P < 0.001$) as well as water temperature (within subjects: $P = 0.032$, between subjects: $P = 0.048$) both within and between individuals. Shorter dives required relatively more energy than longer dives, especially dives of less than 20 s duration. Also, foraging metabolic rate was significantly dependent on body mass ($P = 0.018$). As trends within and between subjects were consistent, data were pooled for analysis. Foraging metabolic rates for the platypus are best predicted by

$$P_{(\mathrm{FORAGE})} = 9.04 - 0.21\ T_{\mathrm{w}} - 0.90\,\mathrm{m} + 109.21\ t^{-1}(n = 555, r^2 = 0.61) \qquad (3)$$

(in W kg $^{-1}$) where T_w = current water temperature (°C), m = body mass (kg) and t = dive duration (s).

To compare the metabolic rates of animals equipped with data loggers and that of animals without data loggers, data were standardised for water temperature, dive duration and body weight. The data loggers did not cause a significant increase in the mean foraging metabolic rate (t-test, $t = 0.55$, $P = 0.297$). To compare males and females we standardised the data for water temperature and dive duration only. Foraging rates for female animals (8.73 W kg^{-1}, SD = 0.22, $n = 6$) were significantly higher than for males (8.14 W kg^{-1}, SD = 0.40, $n = 6$, t-test, $t = -1.84$, $P = 0.047$). However, testing for differences between male and female animals independent of body weight did not find a significant difference in power requirements between the sexes (t-test, $t = 0.24$, $P = 0.407$). Consequently, different power requirements for male and female platypuses relate to differences in body weight rather than physiological differences between the sexes. The mean foraging metabolic rate obtained from 12 platypuses was 8.48 W kg^{-1} (SD = 0.66, $n = 12$, equals 1.52 ml O_2 g^{-1} h^{-1}).

To be able to compare power requirements for underwater swimming in the platypus with other subsurface swimmers, we estimated the metabolic rate for subsurface swimming $P_{(\mathrm{DIVE})}$. In this study, the best estimation of $P_{(\mathrm{DIVE})}$ is the energy requirements of platypuses foraging on the tank bottom (phase-2-behaviour). If we assume that the cost of resurfacing after the dive is negligible due to the positive buoyancy of the animals, we can obtain $P_{(\mathrm{DIVE})}$ following $P_{(\mathrm{DIVE})} = P_{(\mathrm{FORAGE})} - P_{(\mathrm{DESCENT})}/t$, where t is dive duration (s) and $P_{(DESCENT)}$ (J kg^{-1}) is the total cost for diving vertically down to the bottom of the tank (phase-1). The latter behaviour was characterised by powerful strokes with the forefeet and high swimming speeds. Therefore, $P_{(\mathrm{DESCENT})}$ can be best estimated following $P_{(\mathrm{DESCENT})} = P_{(\mathrm{MAX})}\ \mathrm{d}\ \mathrm{v}_{(\mathrm{MAX})}^{-1}$, where $\mathrm{P}_{(\mathrm{MAX})}$ is the highest swimming metabolic rate measured (20.17 W kg^{-1}), $v_{(MAX)}$ is the highest speed observed (0.43 m s^{-1}) and d is the water depth. The mean metabolic rate $P_{(\mathrm{DIVE})}$ for subsurface swimming was 6.71 W kg^{-1} (SD = 0.68, $n = 12$, equals 7.34 W kg$^{-0.75}$ or 1.20 ml O_2 g^{-1} h^{-1}).

Cost of transport (COT, in J N^{-1} m^{-1}) is power (W kg^{-1}) divided by speed (m s^{-1}) and gravitational acceleration (9.81 m s^{-2}) (Videler and Nolet 1990; Fish 2000). COT was obtained from dives performed in the 3-m-long swim canal ($n = 119$, from 12 animals). No food was supplied in the canal to minimise searching behaviour and to restrict behavioural activity to under water swimming only. COT was derived following $\mathrm{COT} = P_{(\mathrm{DIVE})}\ (\mathrm{v}\ g)^{-1}$, where v = speed (m s^{-1}), g is the gravitational acceleration and $P_{(\mathrm{DIVE})}$ is the power for subsurface swimming. Mean COT was 3.98 J N^{-1} m^{-1} (SD = 1.40, $n = 12$) and ranged from 1.85 J N^{-1} m^{-1} at 0.4 m s^{-1} to 5.88 J N^{-1} m^{-1} at 0.1 m s^{-1}. Power input as well as transport costs were significantly dependent on speed ($P < 0.001$; Fig. 2). Data was divided in four speed classes ranging from 0.1 m s^{-1} to 0.4 m s^{-1} for further analysis.

During swimming, power input first increases and then remains stable with rising speed (Hind and Gurney 1997; Videler and Nolet 1990). As swimming speed rises further, hydrodynamic drag, which increases roughly in proportion to the square of speed, becomes the predominant factor. The power to overcome hydrodynamic drag increases with the third power of speed (Schmidt-Nielsen 1995) which is why we used a third degree polynomial function to regress power input during subsurface swimming against speed (see for comparison Culik and Wilson 1994; Bethge et al. 1997; Borgwardt and Culik 1999) yielding $P_{(\mathrm{DIVE})} = 236.14\ \mathrm{v}^3 - 167.84\ \mathrm{v}^2 + 35.51\ \mathrm{v} + P_{(\mathrm{REST})[\mathrm{water}]}$ where v = swim speed and $P_{(\mathrm{REST})[\mathrm{water}]}$ = power input during rest at the water surface (4.81 W kg^{-1}), (Fig. 2). The corresponding curve fit for COT is:

$$COT = 24.07v^2 - 17.12v + 3.62 + 0.49v^{-1}(n = 4, r^2 = 0.90) \qquad (4)$$

At the preferred swim speed in the canal of 0.2 m s^{-1} COT was 3.61 J N^{-1} m^{-1}. However, to compare the platypus to other subsurface swimmers of different size, we determined the minimum COT for the platypus, which is a constant for each animal and allows direct comparison of different locomotor strategies (Taylor et al. 1970; Tucker 1970; Schmidt-Nielsen 1972; Videler and Nolet 1990; Fish 1992). Minimum COT for subsurface swimming platypuses derived from Eq. 4 was 1.85 J N^{-1} m^{-1} (equals 18.12 J kg^{-1} m^{-1}) at a swim speed of 0.40 m s^{-1} (Fig. 2).

Metabolic rate and COT for walking

Platypuses would only walk on the treadmill over a narrow range of low walking speeds (0.2–0.3 m s^{-1}). At

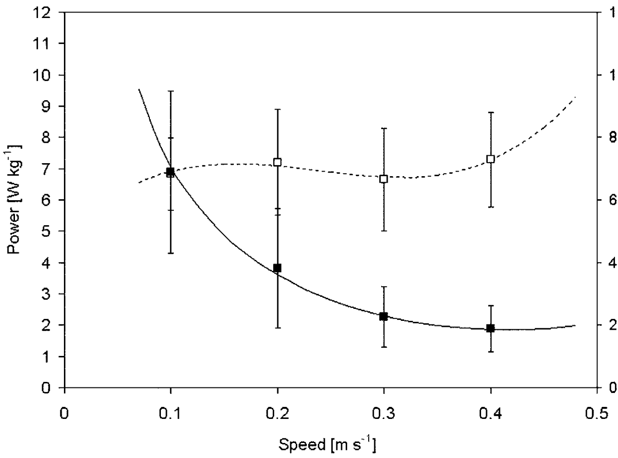

Fig. 2 Modelled cost of transport (COT; *solid line*) and power input (*dotted line*) of platypuses swimming under water at various speeds in a swim canal, plotted as a function of swim speed. COT shows a minimum of 1.85 J N^{-1} m^{-1} at 0.4 m s^{-1}. Means ± SD shown

lower speeds the animals tried to escape from the metabolic chamber. At higher speeds they ceased walking in most cases and experiments had to be abandoned. The only gait used by the platypuses was walk. Metabolic rates $P_{(\mathrm{WALK})}$ were obtained from eight animals and ranged between 8.80 W kg^{-1} (at 0.2 m s^{-1}, SD = 0.96, $n = 8$) and 10.56 W kg^{-1} (at 0.3 m s^{-1}, SD = 0.93, $n = 8$). Walking metabolic rates were regressed against speed and were found to be significantly dependent on walking speed ($P < 0.001$). Assuming a linear increase in metabolic rate with increasing speed for the platypus as demonstrated by Fish et al. (2001), walking metabolic rates for the platypus can be estimated following

$$P_{(\mathrm{WALK})} = 5.22 + 17.74\ \mathrm{v}(n = 16, r^2 = 0.82) \qquad (5)$$

where v = walking speed (m s^{-1}) and $P_{(WALK)}$ = the metabolic rate for walking (W kg^{-1}). COT was derived following COT = $P_{(\mathrm{WALK})}$ $(\mathrm{v}\ g)^{-1}$ where v = speed (m s^{-1}), g is the gravitational acceleration and $P_{(\mathrm{WALK})}$ is the metabolic rate for walking (Videler and Nolet 1990). COT ranged from 4.47 J N^{-1} m^{-1} at a speed of 0.2 m s^{-1} to 3.58 J N^{-1} m^{-1} at 0.3 m s^{-1}.

Discussion

Resting metabolic rates

Our results for the resting metabolic rate in air of the platypus are consistent with the results of Grant and Dawson (1978a; 2.28 W kg$^{-0.75}$ at 26 °C and 2.21 W kg$^{-0.75}$ at 25 °C respectively). Similarly, the gradual increase in metabolism with decreasing temperature observed in this study is consistent with data recorded by Grant and Dawson (1978a), Smyth (1973) and Martin (1902). In this study, metabolism in air at 10 °C increased to 1.5-times the resting level while immersion in water of 9 °C raised the metabolism of the platypus to a maximum of 3.1-times RMR (6.98 W kg$^{-0.75}$). Grant and Dawson (1978a) reported an increase in metabolism of 3.2-times RMR during immersion in water of 5 °C and a maximum resting rate of 7.0 W kg$^{-0.75}$. While resting metabolic rates in air were measured for fasted animals, resting metabolic rates in water were obtained from animals which had access to food in the swim tank. An effect of feeding on the resting metabolic rates in water cannot be ruled out. However, MacArthur and Campbell (1994) reported that, in aquatic trials with muskrats, average steady-state oxygen consumption rates of fed animals were similar to values recorded from fasted animals, suggesting substitution of heat increment of feeding mainly for thermoregulatory heat production in semiaquatic species.

'Wedging' rates calculated in this study are well below the resting rates of platypuses on the water surface at similar temperatures. Although the body is totally submerged while 'wedging' and heat loss is likely to be higher than on the water surface, metabolism increased only to a maximum of two-times RMR on land (4.1 W kg^{-1} at 9 °C). This indicates a very effective mechanism of decreasing metabolism during 'wedging' and supports the work of Grant and Dawson (1978a) and Evans et al. (1994) who reported adaptations in the platypus to greatly restrict heat loss and a profound bradycardia, especially in long dives of over 1 min duration. We observed platypuses 'wedging' under water for up to 5 min. Jones et al. (1987) reported 'wedging' in excess of 6 min in captive platypuses while Evans et al. (1994) recorded 'wedging' of up to 11 min duration. The reported physiological adaptations in combination with the low metabolic rate could explain why platypuses are able to stay inactive under water for extended periods of time.

Resting rates of monotremes are reportedly lower compared to those of marsupials and most eutherian animals (Dawson and Hulbert 1970; Grant and Dawson 1978a). However, in this study, the platypus had a metabolic rate which was only 4% lower than that predicted for marsupials in general by Dawson and Hulbert (1970) and 33% respectively 35% lower than that predicted for an eutherian mammal of similar size by Dawson and Hulbert (1970) and Kleiber (1932). Irving (1973) proposed that semiaquatic and aquatic mammals have higher SMRs than terrestrial mammals to compensate for heat loss in water. Indeed, the metabolism of a number of semiaquatic species has been found to be considerably higher than that of terrestrial species of the same size (Morrison et al. 1974; Pfeiffer and Culik 1998; Borgwardt and Culik 1999). The results for the platypus are in line with these findings. RMR of the platypus was 165% and 132% higher than that of its terrestrial relatives, the long-beaked and the short-beaked echidna, respectively (Schmidt-Nielsen et al. 1966; Augee 1976; Dawson et al. 1979).

Active metabolic rate in water

The platypus resembles small mammals and most diving birds in diving after inspiration (Evans et al. 1994). Oxygen can be stored in the lungs, in the blood and in the tissues of the animal and can then be made available during diving. The amount of oxygen stored and the energy consumption under water determine the time the animal can remain underwater before oxygen stores are fully utilized, i.e. the aerobic dive limit (ADL). A calculation of ADL from the product of the oxygen stores prior to a dive (25 ml; Evans et al. 1994) and the energy equivalent for oxygen (20.11 kJ l^{-1} O$_2$) divided by the power requirements for foraging $P_{(\mathrm{FORAGE})}$ produces a value of 59 s. This result is consistent with the results of Evans et al. (1994) who suggested that during active diving oxygen stores of the platypus would be depleted after 60 s.

Only few active dives reported from the wild exceed this ADL (Kruuk 1993; Otley et al. 2001; P. Bethge, unpublished data) which suggests that there is little need for anaerobic metabolism during normal diving behaviour in the platypus. This view is supported by the characteristics of platypus skeletal muscle. Evans et al. (1994) found that the distribution and properties of LDH isoenzymes in skeletal muscle of the platypus do not suggest heavy dependence on anaerobic glycolysis. Also, the ability of platypus muscles to buffer metabolic acids that accumulate during anaerobiosis is low relative to other diving mammals (Evans et al. 1994).

Platypuses spend, on average, 13 h a day foraging (Otley et al. 2001; P. Bethge, unpublished data) hence diving and the costs involved are crucial to the energy budget of the platypus. Fish et al. (1997) investigated the metabolism of swimming in the platypus by measuring oxygen consumption in a recirculating water flume. The mean metabolic rate of their animals whilst swimming against a constant water current of 0.45–1.0 m s^{-1} was 5.14 W $kg^{-0.75}$ at a water temperature of 15 °C (Fish et al. 1997). This is considerably lower than the rate for submerged swimming $P_{(\mathrm{DIVE})}$ derived in this study (7.34 W $kg^{-0.75}$). The difference can partly be explained by the fact that the rates reported here include the costs for limited searching behaviour on the tank bottom. Surprisingly however, the active metabolic rate estimated by Fish et al. (1997) is 14% lower than the resting metabolic rate of platypuses in water for a comparable water temperature determined by Grant and Dawson (1978a; 6.0 W $kg^{-0.75}$ at 15 °C, derived from graph). This suggests that metabolic rates during swimming might have been underestimated by Fish et al. (1997). Their low rates are also unexpected if we take into account that animals in their study temporarily swam on the water surface which is generally regarded as more costly for semiaquatic mammals (Williams 1989).

Compared to swim flumes where animals have to maintain an unnatural position or a certain speed, the swim tank used in this study allowed the platypuses to select their own swimming speed and dive duration and to forage voluntarily while all activities and gaseous exchange could be closely monitored (see also Culik and Wilson 1991; Culik and Wilson 1994; Bethge et al. 1997). The derived foraging metabolic rate, $P_{(\mathrm{FORAGE})}$, includes the costs of diving to the bottom of the tank (phase-1-behaviour), of the typical searching behaviour and food intake (phase-2) as well as of resurfacing after the dive (phase-3). Therefore, we believe that Eq. 3 provides a good prediction of the minimal metabolic requirements of platypuses foraging in the wild.

As expected, foraging rates of the platypus were found to be dependent on body weight and water temperature with low water temperatures resulting in higher rates and smaller individuals using more energy per unit body mass than larger animals due to a higher surface to volume ratio (Schmidt-Nielsen 1984). Also, foraging rates of the platypus were found to be dependent on dive duration with short dives resulting in relatively higher foraging costs, especially dives of less than 20 s duration. Part of these higher costs may be explained by less metabolic depression in short dives. Evans et al. (1994) reported a marked bradycardia for platypuses while diving and found that heart rate fell less and was more erratic in shorter dives. Similarly, MacArthur and Karpan (1989) observed an increase in the extent of bradycardia with the period of submergence in muskrats. In addition, the observed increased energy consumption by platypuses making short dives can be explained by the high percentage of time spent on the costly descent (phase-1 behaviour). For example, in this study it was observed that in a 15-s dive platypuses spent nearly one fourth of their total foraging costs on the dive to the bottom of the tank. These results suggest that platypuses are likely to prefer shallow streams and pools for foraging and that they have a preference for longer dive durations, a view that is supported by observations from the wild. Only a low percentage of dives reported from the wild are shorter than 20 s (Kruuk 1993; Evans et al. 1994).

Calculation of minimal COT provides a common basis for comparing COT between animals of different size. With this approach the efficiency of different locomotor modes can be compared without consideration of velocity (Tucker 1970; Schmidt-Nielsen 1972; Videler and Nolet 1990; Fish 1992; Williams 1998). Tucker (1970) defined an optimum swimming speed where the amount of work per metre reaches a minimum. Often, the lowest costs occur at the mid-range of routine speeds used by an animal and are within a trough of a U-shaped curve that relates transport cost to swimming speed (Williams et al. 1987; Williams 1989). COT of the platypus was lowest with 1.85 J N^{-1} m^{-1} at a swim speed of 0.4 m s^{-1} (Fig. 2). This speed is the optimal cruising speed for submerged swimming platypuses and is slightly lower than the optimum speed predicted by Videler and Nolet (1990) for a submerged swimmer with the body mass of a platypus (0.55 m s^{-1}).

Minimum COT derived in this study was more than three-times higher than the minimum COT determined by Fish et al. (1997; i.e. 0.51 J N^{-1} m^{-1} at a speed of 1 m s^{-1}). For the reasons discussed above we believe that COT was underestimated in their study. In addition, Fish et al. (1997) did not observe a change in metabolic rate in the platypus over the speed range tested which is rather unexpected for swimming animals (Videler and Nolet 1990; Hind and Gurney 1997). Also, the behavioural observations made in this study and a number of other studies (Evans et al. 1994; Manger and Pettigrew 1995) indicate that the swimming speeds chosen by Fish et al. (1997; 0.45–1.0 m s^{-1}) might have been far too fast for normal platypus behaviour. Interestingly, platypuses in this study chose to swim at a mean speed of only 0.2 m s^{-1}, which is markedly slower than the optimal speed predicted (0.4 m s^{-1}).

This suggests that platypuses rarely optimise for speed while foraging but rather spend their time performing a thorough search of an area. Optimising the time under water rather than the efficiency of locomotion seems ecologically reasonable when the feeding and foraging habits of the animal are taken into account (Grant 1995).

Active metabolic rate on land

Although mainly aquatic, platypuses are known to walk over land for extended periods of time, for example to get from one water body to the other, to by-pass dams or to avoid drought or flood conditions (Grant 1995). Consistent with results obtained for Australian water rats (Fish and Baudinette 1999) and mink (Williams 1983b), platypuses showed higher power requirements for walking than predicted for specialised walkers (Taylor et al. 1982). At the observed speeds of 0.2 m s^{-1} and 0.3 m s^{-1}, walking metabolic rate was 19% and 27% higher, respectively, than that predicted by Taylor et al. (1982) for a terrestrial mammal of similar size.

Fish et al. (2001) reported walking metabolic rates for the platypus of 3.65 W kg^{-1} and 4.22 W kg^{-1} at speeds of 0.2 m s^{-1} and 0.3 m s^{-1}, respectively. These rates amount to only half the rates measured in this study and are even lower than those of similarly sized specialised walkers of eutherian origin (Taylor et al. 1982). Also, minimum transport costs for walking reported by Fish et al. (2001) were lower than those for specialised walkers (Taylor et al. 1982). These results are rather unexpected. Limb orientations and limb movements of locomoting monotremes have been claimed to be primitive and essentially the same as those of lepidosaurian reptiles (Pridmore 1985). The platypus shows a unique locomotor movement on land, with humeral long-axis rotation, horizontal retraction of humerus and femur and distally heavy limbs specialised for digging. The short legs and the flattened body morphology produce problems of body support and restrictions in stride length not experienced by longer legged vertebrates. Despite lower maintenance costs, these limitations and the semiaquatic lifestyle of the platypus are likely to be reflected in elevated energetics costs for walking compared to locomotor specialists. The results of this study confirm this suggestion.

Comparison with other mammalian swimmers and divers

Costs for subsurface swimming of the platypus were found to be 51% lower than predicted for a eutherian mammal of comparable body size and lifestyle (for comparison, published data were regressed against body weight; Table 1). Muskrats, for example, (body weight: 1 kg; MacArthur and Krause 1989) have an active metabolic rate nearly two-times as high as that of the platypus. Asian small-clawed otters (body weight: 3.1 kg; Borgwardt and Culik 1999) swimming under water expend energy at a rate 2.1-times that of the platypus. The same can be said for the walking platypus. While mink [$P_{(\mathrm{WALK})} = 13.4 + 11.26$ v; Williams 1983b] and Australian water rat [$P_{(\mathrm{WALK})} = 14.0 + 11.56$ v; Fish and Baudinette 1999] showed nearly similar power requirements for walking, platypuses expended energy at only half the rate over the range of speeds investigated in this study. Also, resting rates of the platypus in air and water were found to be 55% and 56% lower, respectively, than those predicted for its eutherian counterparts (Table 1). Thus, resting as well as walking and submerged swimming platypuses appear to utilise energy at only half the rate of semiaquatic eutherians of comparable body size.

In contrast, minimal transport costs for submerged swimming platypuses were similar to those obtained for semiaquatic eutherians, especially those obtained for otter species by Borgwardt and Culik (1999), Pfeiffer and Culik (1998) and Williams (1989; Fig. 3). An allometric expression,

$$COT = 2.12\ \text{mass}^{-0.373} (r^2 = 0.97), \tag{6}$$

was derived which describes the COT for semiaquatic mammals ranging in size from 1.43 kg (platypus) to

Table 1 Energetic requirements of semiaquatic mammals during swimming and comparison to the platypus. Data on *muskrats* from MacArthur and Krause (1989), on *Asian small clawed (ASC) otters* from Borgwardt and Culik (1999), on *river otters* from Pfeiffer and Culik (1998), on *beavers* from Allers and Culik (1997), on *sea otters* from Williams (1989) and Morrison et al. (1974), on *platypuses* from this study

	Mass (kg)	RMR (W kg^{-1})	Rest in water (W kg^{-1})	Subsurface swimming (W kg^{-1})	Cost of transport (COT; J $N^{-1}m^{-1}$)	Swim speed (m s^{-1})	Locomotor cost (LC; J $N^{-1}m^{-1}$)
Muskrat	1.0	4.39	N/A	12.49	N/A	N/A	N/A
ASC Otter	3.1	5.03	9.1	14.2	1.47	0.9	0.45
River Otter	6.2	4.1	6.4	12.1	0.95	1.3	0.45
Beaver	18.6	1.58	2.31	3.18	0.36	0.9	0.10
Sea Otter	19.9	3.72	4.58	5.95	0.76	0.8	0.18
Regression (for Eutherians)		$P_{(\mathrm{REST})\mathrm{AIR}} = -0.11 \times \text{mass} + 4.85$ $r^2 = 0.56$	$P_{(\mathrm{REST})\mathrm{WATER}} = -0.30 \times \text{mass} + 9.18$ $r^2 = 0.80$	$P_{(\mathrm{DIVE})} = -0.51 \times \text{mass} + 14.51$ $r^2 = 0.89$			
Prediction for Platypus	1.43	4.69	8.75	13.79			
Platypus (this study)	1.43	2.08	3.91	6.71	1.85	0.4	0.85
Platypus/Prediction (%)		44	45	49			

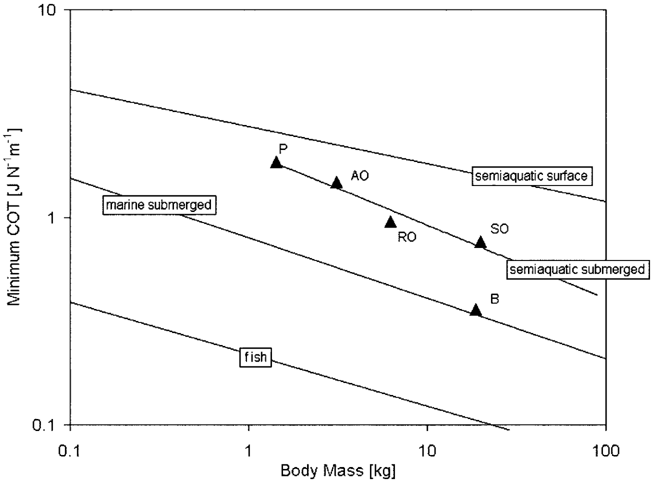

Fig. 3 Minimal transport costs of different semiaquatic swimmers (▲) plotted as a function of body mass (log/log plot). Submerged swimming data on Asian small-clawed otters (*AO*) from Borgwardt and Culik (1999), on river otters (*RO*) from Pfeiffer and Culik (1998), on sea otters (*SO*) from Williams (1989) and on beavers (*B*) from Allers and Culik (1997). Data on platypuses (*P*) from this study. Modelled transport costs in surface swimming semiaquatic mammals (Williams 1989), in marine mammals (Williams 1998) and in Fish (Salmon; Brett 1964) are shown for comparison. Model for COT in submerged swimming semiaquatic mammals (beaver excepted): COT = 2.12 mass$^{-0.373}$

19.9 kg (sea otter) (Fig. 3). Results obtained for the beaver by Allers and Culik (1997), however, do not fit this allometric model.

Transport costs derived for the walking platypus (3.58 J N^{-1} m^{-1}) were even higher than minimum transport costs reported for semiaquatic eutherians (mink: 1.51 J N^{-1} m^{-1}; Williams 1983b; Australian water rat: 2.08 J N^{-1} m^{-1}; Fish and Baudinette 1999). However, walking speeds of platypuses were very low in this study and COT measured here is not likely to be the minimum COT for walking in the species.

Transport costs can be described as the sum of maintenance costs (MC) and locomotor costs (LC) where – for swimming animals – MC is the cost for resting in water and LC is the energy expended for swimming performance (Williams 1989; Williams 1998). Table 1 shows a comparison of MC and LC for submerged swimming platypuses (this study) and eutherian semiaquatic animals. LC of the platypus amount to 46% of total COT and are much higher than the relative LC of the other animals. In effect, these LC costs make up for the advantages the platypus experiences through lower MC.

We suggest that the high LC of the platypus are a consequence of its small body size and the low under water swimming speed which are likely to result in increased drag. Bannasch (1995) showed that for Pygoscelid penguins friction drag is higher at low speeds or smaller body sizes. Also, small animals do not seem to fit the allometric models (Culik and Wilson 1994; Williams 1998). In little penguins engaged in subsurface swimming for example, COT was twice as high as predicted (Bethge et al. 1997).

In addition, platypuses use a different swimming mode from otters. Like most other semiaquatic eutherians (also beaver *Castor canadensis*, muskrat *Ondata zibethicus*), otters paddle with their hindlimbs in a vertical plane beneath the body (Fish 1993). The platypus, however, uses pectoral rowing (Howell 1937; Grant 1989), a mode used by only a few other semiaquatic mammals including the polar bear *Ursus maritimus* and the ferret *Mustela putorius*. Both modes of locomotion rely on drag-based oscillating appendages, which provide thrust by entraining a large volume of water during stroke. However, this study suggests that the paddling mode of the platypus might be less efficient than the hind-limb propulsion showed by the otter species.

Compared to animals with different strategies of locomotion in water, i.e. surface paddlers and specialised subsurface swimmers, the platypus, as expected, exhibits intermediate costs of locomotion (Fig. 3). COT determined in this study was 28% lower than transport costs predicted from Williams (1989) for surface-swimming semiaquatic mammals (COT = 2.73 M$^{-0.18}$) but 180% and 158% higher than transport costs predicted by Culik and Wilson (1994) for subsurface-swimming homeotherms (COT = 0.71 M$^{-0.205}$) and by Williams (1998) for marine mammals (COT = 0.79 M$^{-0.29}$), respectively. The platypus has transport costs nine-times greater than the minimum COT for a fish of equivalent body mass (Brett 1964; COT = 0.22 M$^{-0.25}$).

To conclude, energetic demands of the platypus show the typical characteristics of semiaquatic mammals. Active and inactive metabolic rates were found to be higher than those of terrestrial species of comparable body size. As might be expected for their position between terrestrial and aquatic specialists, the diving platypus is clearly more efficient than surface paddling homeotherms but has higher energy requirements for underwater locomotion than specialised divers. Williams (1998) suggested that the transitional lifestyle of semiaquatic mammals incurs costs that are 2.4 to 5.1-times higher than for locomotor specialists. With increased specialisation of one locomotor mode, a subsequent reduction in locomotor agility of alternate modes occurs (Williams 1983a). As a result, foraging is preferentially limited to a single habitat, which, in case of the platypus, is clearly the aquatic environment where foraging occurs and food is collected.

Compared to eutherian mammals of comparable lifestyle, however, power requirements of the platypus were low. Active metabolic rates in water at preferred speed as well as walking and maintenance costs of the platypus were on average only half as high as those of semiaquatic eutherians – energetic advantages the platypus possibly experiences because of its monotreme origin.

Surprisingly, however, transport costs of the animal under water, i.e. the degree of aquatic specialisation, was found to be comparable to that of otter species. Low locomotor speeds, a small body size and the lifestyle of the platypus are likely reasons for this apparent contradiction. While foraging under water, the animal has to optimise for bottom time rather than for speed and therefore efficiency of locomotion. However, comparable minimum costs of transport of the platypus and its eutherian counterparts might also indicate a general limitation in the efficiency of locomotion in semiaquatic mammals. Even with a generally lower metabolism, the platypus seems to encounter comparable energetic problems to its eutherian counterparts during swimming. This suggests that, confronted with the need to perform in water and on land, locomotor efficiency of semiaquatic animals might have reached a limit for energetic optimisation due to limits in the mechanics of locomotion.

A comparable limitation of energetic optimisation was proposed for specialised mammalian divers and runners by Williams (1998) who argued that mammals had to vault an energetic hurdle encountered during the semiaquatic state in the evolution from terrestrial specialists to aquatic specialists. This study supports the view that this energetic hurdle is still challenging today's semiaquatic mammals. The very different physical conditions in the two media, land and water, impose the same increased energetic demands on semiaquatic mammals regardless of their taxonomic origin.

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