

ENERGETICS OF SWIMMING BY THE PLATYPUS *ORNITHORHYNCHUS ANATINUS*: METABOLIC EFFORT ASSOCIATED WITH ROWING

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Summary

The metabolism of swimming in the platypus *Ornithorhynchus anatinus* Shaw was studied by measurement of oxygen consumption in a recirculating water flume. Platypuses swam against a constant water current of 0.45–1.0 m s⁻¹. Animals used a rowing stroke and alternated bouts of surface and submerged swimming. Metabolic rate remained constant over the range of swimming speeds tested. The cost of transport decreased with increasing velocity to a minimum of 0.51 at 1.0 m s⁻¹. Metabolic rate and cost of transport for the platypus were lower than values for semiaquatic mammals that swim at the water surface using a paddling mode. However, relative

to transport costs for fish, the platypus utilized energy at a similar level to highly derived aquatic mammals that use submerged swimming modes. The efficient aquatic locomotion of the platypus results from its specialised rowing mode in conjunction with enlarged and flexible forefeet for high thrust generation and a behavioral strategy that reduces drag and energy cost by submerged swimming.

Key words: platypus, *Ornithorhynchus anatinus*, swimming, metabolism.

Introduction

The platypus *Ornithorhynchus anatinus* demonstrates highly specialized habits and anatomy adapted to a semiaquatic existence. Its fur is extremely fine and dense, insulating the body and providing buoyancy in water (Grant and Dawson, 1978). Broad webbed feet are used for swimming and maneuvering in the water. A visual examination showed that the platypus swims by alternate rowing motions of its forelimbs (Howell, 1937; Grant, 1989), which are oriented in the horizontal plane. During swimming, the hindfeet are held immobile against the sides of the body and together with the broad, compressed tail are used solely for maneuvering (Howell, 1937).

Typically, semiaquatic mammals (e.g. beaver *Castor canadensis*, muskrat *Ondatra zibethicus* and otter *Lutra canadensis*) swim using their hindlimbs in a vertical plane beneath the body in the paddling mode (Fish, 1993). Both paddling and rowing motions are considered to be inefficient, because only half the stroke of the limbs is used to generate forward propulsion (thrust), whereas the other half of the stroke, which is used to reposition the limb, increases the resistance to forward movement (drag), thus reducing the net thrust generated (Howell, 1937; Fish, 1984, 1993). Animals which use paddling modes have high energy costs for

swimming as determined from measurement of oxygen consumption (Holmer, 1974; Fish, 1982; Baudinette and Gill, 1985; Williams, 1983, 1989). When compared with body drag or mechanical power output, the high energy costs of paddling have translated into aerobic efficiencies of no more than 5%, which is lower than for the highly derived swimming modes of aquatic mammals (Fish, 1993).

The purpose of the present study was to examine the energetics of rowing by the platypus. The relationship between metabolic energy input and swimming effort was determined by measurement of oxygen consumption of animals swimming against a constant current at different velocities in a water flume. The platypus is the only mammal to swim by rowing motions of the pectoral appendages. Comparisons of locomotor efficiency with other mammalian swimmers were made possible by calculation of cost of transport.

Materials and methods

Animals

Six adult platypuses *Ornithorhynchus anatinus* Shaw were netted in creeks near Eildon in north-eastern Victoria, Australia, under a permit from the State Department of

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Conservation and Land Management. Fyke or eel nets were used in smaller creeks and gill nets were used to take animals from larger bodies of water. The latter nets were monitored continuously, and the animals were removed within 1 min of becoming entangled. Under the conditions of the collection permit, the animals could only be held for a period of 8 h as a result of their marked adrenocortical response to the stress of capture (McDonald *et al.* 1992). Animals were subsequently released at the capture site.

All experiments were conducted between 22:00 and 04:00 h, a period encompassing the normal activity periods of the animals. Each of the animals was swum at either three or four speeds spaced at approximately 120 min intervals over the holding period. A swimming period lasted for 10–15 min.

Water flume

Swimming metabolic studies were conducted in a water flume similar in design to those used by Fish (1982) and Williams (1983). The flume was constructed from a flat fiberglass tank of dimensions 3.1 m×0.7 m×0.3 m. The tank was divided longitudinally to form a working section (1.0 m×0.4 m×0.3 m) and a return section through which water was circulated using a variable-speed electric outboard motor (Mercury; model T2400) connected to a 12 V battery. Using this device, flows of up to 1.0 m s⁻¹ were achieved. Turbulence in the working section was reduced using a plastic grid of 12 mm×12 mm squares in which the ratio of width to length of the elements was 1:8. In addition, the area of the return section downstream of the motor was covered with a sheet of plywood to prevent wave formation.

Water flow velocity (U , in m s⁻¹) in the working section was measured using a calibrated current meter (Global Flow Probe; Global Water, Fair Oaks, CA, USA). Profiles of water flow did not show significant variation or turbulence in the region in which the animals swam.

Metabolic measurements

The top of the working section consisted of a 5 l respiratory chamber with a slanted roof formed by a clear acrylic plastic cover bounded by flexible side panels. Water levels were maintained above the lower extremities of the chamber, creating a sealed airspace above the animal's head. Room air was drawn through inlet and outlet ports placed at opposite sides of the chamber at a regulated flow rate of 15 l min⁻¹.

Measurements of oxygen consumption were made at water temperatures between 15 and 16 °C. The flow of gas from the respiratory chamber was regulated by a mass-flow controller (model 840, Sierra Instruments, Monterey, CA, USA) calibrated against a Brooks volumeter. A subsample of the exhalant stream was scrubbed of carbon dioxide and water, respectively, in an Ascarite and Drierite (CaSO₄) column and pumped into an oxygen analyser (Applied Electrochemistry, model S-3A) for determination of the fractional concentration of oxygen measured at ±0.02% O₂. The output from the analyser was digitised (Universal Interface, Sable Systems, Las Vegas, NV, USA) and analysed using DATACAN V software

(Sable Systems). In most cases, steady-state plateaus of at least 4 min during which the platypus swam on the surface were used for analysis, but at higher swimming speeds the frequency of diving increased in some individuals and an integration algorithm was applied to the data. During analysis, any drift in the O₂ monitoring system was corrected by linear interpolation between the initial and end baseline readings, which were recorded before and after introduction of the platypus into the respiratory chamber, respectively.

The rate of oxygen consumption (\dot{V}_{O_2}) was calculated according to:

$$\dot{V}_{O_2} = \frac{\dot{V}_E(F_{IO_2} - F'_{EO_2})}{1 - F_{IO_2} + RQ(F_{IO_2} - F'_{EO_2})}, \quad (1)$$

where \dot{V}_E is the rate of airflow out of the respiratory chamber, F_{IO_2} is the fractional concentration of O₂ entering the chamber, F'_{EO_2} is the fractional concentration of O₂ leaving the chamber, and RQ is the respiratory quotient (Withers, 1977). RQ was assumed to be 0.8. The rate of O₂ consumed at STPD, representing metabolic rate, was converted to its energetic equivalent using a conversion factor of 20.1 J ml⁻¹ O₂.

Cost of transport (COT) can be used to assess directly the efficiency of different swimming modes from determinations of metabolic effort (Tucker, 1970; Schmidt-Nielsen, 1972; Fish, 1992). COT is the metabolic cost used to move a unit mass over a given distance, and COT is inversely proportional to efficiency (Tucker, 1970). COT was calculated as:

$$COT = MR(MgU)^{-1}, \quad (2)$$

where MR is the metabolic rate in J s⁻¹, M is body mass in kg, and g is the gravitational acceleration of 9.8 m s⁻² (Videler and Nolet, 1990). The units of COT are J N⁻¹ m⁻¹, which is dimensionless.

Stroke frequency determinations

To determine the stroke rate of the platypus, a video camera (Panasonic Camcorder, model PV-5100) was mounted above the working section of the flume. Video tapes were recorded at 60 Hz. Lighting was provided by a single floodlamp positioned behind the working section. The floodlamp was turned on after at least 4 min of undisturbed swimming by the platypus.

Sequential frames of video tape (1/30 s) were viewed using a Panasonic AG-7300 video recorder. Video records were chosen for analysis only if the animal swam continuously for at least two stroke cycles, the animal was not interfered with by the water flume (i.e. its forefeet did not contact the walls, floor or metabolic hood), and the animal maintained position in the flume without anterior or posterior displacement.

Results

Three male and three female platypuses were tested. Mean body mass was 1.52±0.37 kg (mean ± s.d.) with a range of 1.11–2.28 kg.

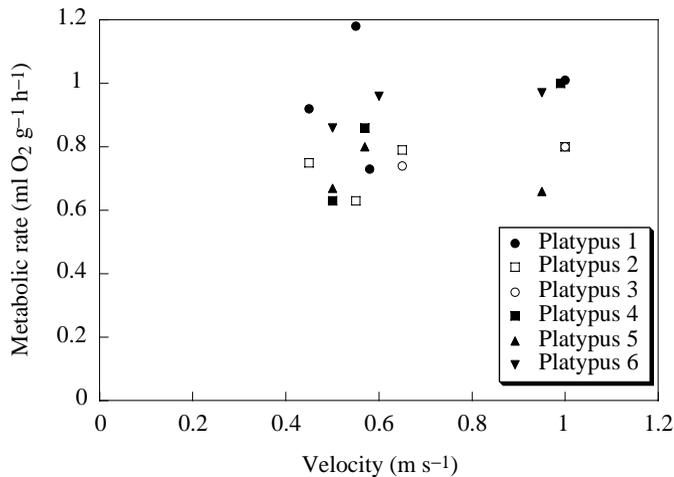


Fig. 1. Mass-specific oxygen consumption of six platypuses as a function of swimming velocity (U). Data points for each individual platypus are shown.

In the water flume, platypuses alternated bouts of surface and subsurface swimming over a range of velocities from 0.45 to 1.0 m s^{-1} . No change in body orientation over this speed range was observed which could affect drag. Animals were easily able to match the speed of the water current. Periods were observed in which the animals were able to swim faster than the highest water speed in the flume. Platypuses swam as described previously (Howell, 1937) using alternate rowing motions of the forelegs to swim against the water flow. Occasionally, when accelerating, the platypus stroked its forelegs simultaneously before returning to alternating strokes.

Diving to exploit lower velocity profiles within the flow tank is a possibility in experiments such as these. This behavior would effectively alter the speed at which the minimum metabolic cost occurred. However, our observations suggest that platypuses were neither diving deeply nor attempting to

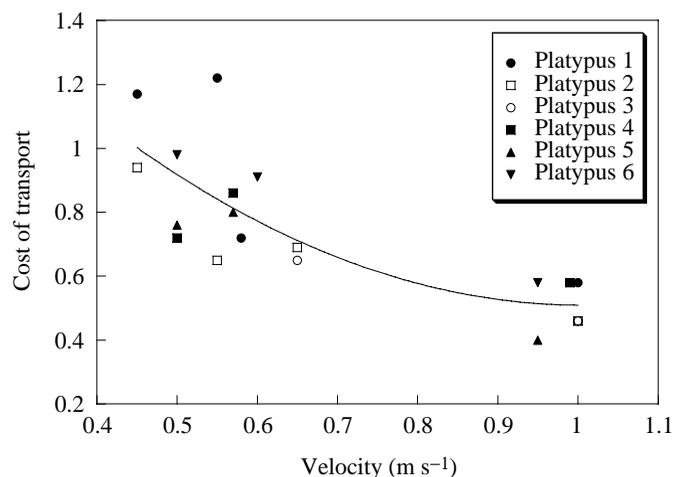


Fig. 2. Dimensionless cost of transport (COT) versus swimming velocity (U) in six platypuses. Data points for each individual platypus are shown. The line was fitted to a second-order polynomial as $\text{COT} = 2.12 - 3.20U + 1.59U^2$.

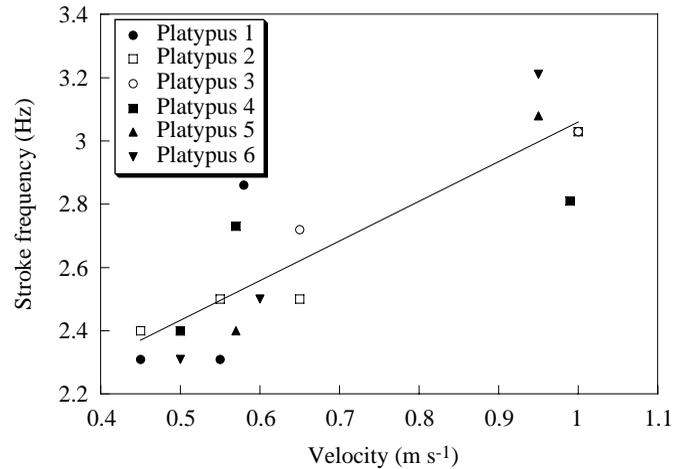


Fig. 3. Stroke frequency (f) versus swimming velocity (U) in six platypuses. Data points for each individual platypus are shown. The line has the equation $f = 1.80 + 1.26U$.

exploit low velocity profiles at the bottom of the working section.

Continuous traces of oxygen consumption over time were interrupted when the platypus was swimming submerged. The rate of oxygen consumption for individual animals showed a 6.7–58.7% increase over the range of swimming speeds investigated, with the exception of one platypus which exhibited a 1.5% decrease in metabolic rate with increasing U . The pooled metabolic data showed that there was no significant change ($r = 0.23$; $d.f. = 17$; $P > 0.1$) in metabolic rate with changes in U (Fig. 1). The mean active metabolic rate was $0.83 \pm 0.14 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ (mean \pm S.D.).

COT decreased curvilinearly with increasing U (Fig. 2). The data were significantly correlated ($r = 0.79$; $d.f. = 17$; $P < 0.001$) with U through a second-order polynomial relationship. The minimum value of COT was 0.51, which occurred at 1.0 m s^{-1} .

Fig. 3 illustrates the relationship between the frequency of the stroke cycle and U . Frequency showed a direct linear relationship with U that was highly significant ($r = 0.89$; $d.f. = 17$; $P < 0.001$).

Discussion

As physical work load due to hydrodynamic resistance increases directly with U , the metabolic work performed by a swimming animal should increase similarly with speed. This relationship is typical for swimming animals (Webb, 1975; Baudinette and Gill, 1985; Fish, 1992). However, there was no change in metabolic rate in the platypus over the range of U tested in the present study. Small increases in metabolic rate occur at low U in other swimming animals (Williams, 1983; Baudinette and Gill, 1985), and the ability of the platypus to swim at speeds faster than those tested here suggests that its metabolic rate may increase at higher speeds. The mean active metabolic rate for platypus was calculated here at $5.14 \text{ W kg}^{-0.75}$, whereas Grant and Dawson (1978) found a maximum metabolic rate of $7.0 \text{ W kg}^{-0.75}$.

The platypus has an active metabolic rate that is low compared with that of other paddle-propulsing semiaquatic mammals of similar body size. Swimming muskrats (*Ondatra zibethicus*) have an active metabolic rate 2–5.1 times that of the platypus (Fish, 1982), whereas swimming mink (*Mustela vison*) expend energy at a rate 4.1–10.7 times greater (Williams, 1983). The platypus also maintains a low resting metabolic rate compared with aquatic eutherian mammals. Grant and Dawson (1978) determined that the resting metabolism of the platypus in air was 35% lower than that of eutherian mammals and was 37–54% lower in water.

The reduced metabolic effort required during swimming by the platypus is reflected in its COT (Fig. 4). The platypus has a COT 2.4 times greater than the minimum COT for a fish of equivalent body mass (Brett, 1964). This is much lower than the equivalent factor for other semiaquatic and terrestrial mammals (Fig. 4), which have a COT 8.9–24.2 times greater than that of fish. However, the relative COT for the platypus is within the range of 1.9–5.6 times greater than fish COT found for highly derived aquatic mammals, including seals, sea lions and whales. These differences may reflect the energy usage dictated by different swimming modes.

The platypus swims by pectoral rowing (Howell, 1937; Grant, 1989). Although some semiaquatic mammals (e.g. polar bear *Ursus maritimus* and ferret *Mustela putorius*) swim exclusively using their pectoral appendages, their strokes are confined to the parasagittal plane similar to the quadrupedal and pectoral paddling used by other semiaquatic mammals (Flyger and Townsend, 1968; Fish, 1993). An examination of paddling has shown these modes to be inherently inefficient (Fish, 1992). Energy is lost mainly due to inertial effects, non-thrust-generating movements during the power stroke and increased drag while repositioning the appendage during the recovery stroke. These losses translate into aerobic efficiencies (the energy needed to provide thrust divided by the total metabolic input) of no greater than 5% and mechanical efficiencies (the energy needed to generate thrust divided by the total mechanical work) of only 33% (Fish, 1992).

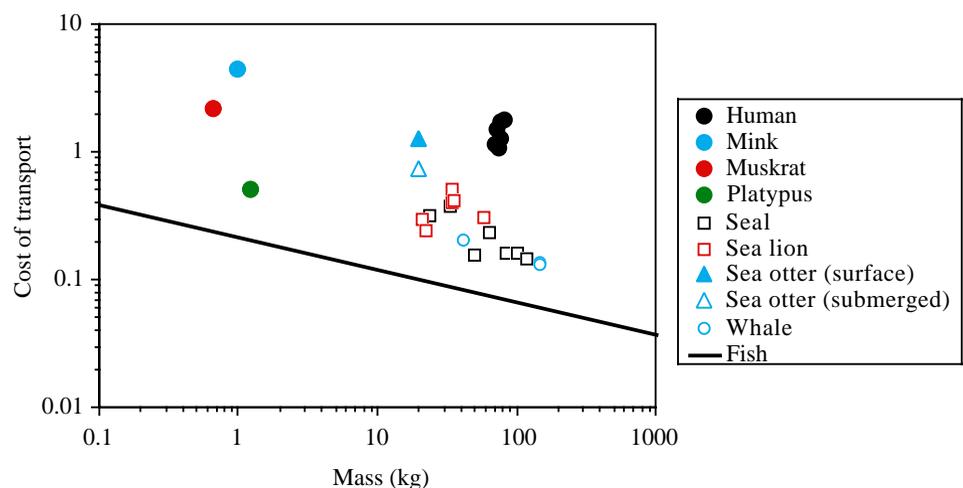
The highly aquatic sea lion *Zalophus californianus* swims

with the foreflippers using a combination of lift-based oscillations and rowing motions (Feldkamp, 1987b). These latter motions produce the greater part of the thrust generated over the stroke cycle. This swimming mode results in aerobic efficiencies of 12–30% and a maximum mechanical efficiency of 80% (Feldkamp, 1987a; Williams *et al.* 1991). Fish (1996) argued that the platypus represents a possible modern analog to an intermediate swimming mode between drag-based paddlers and lift-based pectoral oscillators. Indeed, the pattern for the platypus is more similar to that of the sea lion than that of semiaquatic paddlers. For the platypus and sea lion, stroke frequency increases linearly with increasing U (Feldkamp, 1987b), whereas frequency is independent of U in paddlers (Williams, 1983; Fish, 1984). Although a detailed analysis of the swimming dynamics of the platypus has not been undertaken, the rowing stroke may have a reduced metabolic cost due to efficiencies higher than for semiaquatic paddlers.

The ability to increase swimming efficiency by enhancing thrust generation is associated with the morphology of the propulsive forefeet in the platypus. Webbing on the forefeet is broad and extends beyond the digits during swimming (Grant, 1989). When fully spread (abducted), the forefeet of the platypus have a triangular planform which is the optimal shape for maximizing thrust production during paddling (Blake, 1981). The forefeet constitute the largest surface area of any of the extremities of the platypus, and the combined surface area of the forefeet is 13.6% of total body surface area (Grant and Dawson, 1978). This is comparable with that of sea lion foreflippers, which represent 15.7–16.6% of total body surface area (Feldkamp, 1987a), but is larger than the propulsive hindfeet of semiaquatic rodents, which represent 4.0–6.4% of the wetted surface areas of the body (Mordvinov, 1976). Because a large mass of water can be accelerated by the foot, efficiency will be greater for the platypus than for paddlers with relatively smaller foot areas (Alexander, 1983).

Semiaquatic paddling mammals swim at the surface, but platypuses dive frequently, which can reduce metabolic cost (Fish, 1992; Evans *et al.* 1994). Pronounced bradycardia and the associated hypometabolism during submerged swimming

Fig. 4. Dimensionless cost of transport (COT) versus body mass. Filled symbols represent COT values for paddling semiaquatic mammals when surface swimming, and open symbols represent submerged swimming by aquatic mammals. Data from Holmer (1974); Costello and Whittow (1975); Kruse (1975); Øritsland and Ronald (1975); P. E. DiPrampero, personal communication; Fish (1982); Williams (1983, 1989); Innes (1984); Davis *et al.* (1985); Worthy *et al.* (1987); Feldkamp (1987a) and Williams *et al.* (1992). The solid line represents the extrapolated minimum COT for salmonid fish, from data by Brett (1964).



can offset tachycardia and increased metabolic rate during surface swimming (Castellini, 1988; Williams *et al.* 1991). Like diving pinnipeds and cetaceans, platypuses can dramatically lower heart rate from pre-dive levels of 140–230 beats min⁻¹ to 10–120 beats min⁻¹ during dives (Evans *et al.* 1994). However, the semiaquatic muskrat has a high energetic cost associated with voluntary underwater exercise, despite exhibiting diving bradycardia (MacArthur and Karpan, 1989; MacArthur and Krause, 1989).

An additional energetic benefit of submerged swimming is a reduction in drag (Lang and Daybell, 1963; Baudinette and Gill, 1985; Williams, 1989; Williams *et al.* 1991). When surface swimming, formation of waves augments drag by up to five times (Hertel, 1966), which increases metabolic expenditure and limits swimming speed (Fish, 1982; Williams, 1989). The effect of surface waves is negated when swimming at a depth greater than three times the maximum diameter of the body (Hertel, 1966). Surface-swimming mammals (e.g. human, mink *Mustela vison*, muskrat) have a higher COT than mammals that typically swim submerged (Fig. 4). Sea otters swimming submerged have an oxygen consumption 41% lower than when surface swimming, with an associated 35% reduction in drag (Williams, 1989). Such differences suggest that the locomotor strategy of submerged swimming may result in increased efficiency in the platypus.

In summary, the paradoxical platypus while possessing primitive semiaquatic anatomical structures is a highly specialized swimmer. This animal is capable of efficient aquatic locomotion using a unique swimming mode owing to morphological adaptations for high thrust generation and also to a behavioral locomotor strategy that reduces drag and energy cost. Energetically, the platypus is more similar to highly derived aquatic species than to surface-paddling semiaquatic mammals.

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