

## THE METABOLIC COST OF SWIMMING IN DUCKS

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### INTRODUCTION

Studies on the metabolic rates of animals have typically stressed the measurement of the 'basal' or 'resting' metabolism. From an engineering standpoint, however, the resting level of a system is often of less interest than its maximum output. This point of view may be applied to animal systems as well. In terms of an animal's normal daily activities the minimum metabolism may be of little relevance to the energy the animal requires from its environment. It was the purpose of this study, therefore, to determine the metabolic cost of the performance of an active animal system and the limitations on this performance.

An animal engaged in physical exercise provides a situation from which the output or external work can be used as a gauge of the system's performance. Many studies have been made on men, rats, dogs and domestic animals exercising on various types of apparatus. However, outside this group, relatively few species have been studied in regard to maximum sustained metabolic performance. Unfortunately, in some of these cases the techniques for eliciting physical activity, such as heat or electric shock and measurements taken from animals struggling to free themselves from restraints, are so far removed from reality as to make inferences about the normal performance of the animals of dubious validity.

A further constraint was therefore placed on this work: to study an animal performing some activity common to its usual mode of life and to do so under conditions as free from restraint as possible. Recent studies such as those of Brett (1964, 1967) on young salmon, Moberly (1968) in the iguana, and Lasiewski (1963), LeFebvre (1964) and Tucker (1966, 1968) on flying birds are examples of this type of study.

The swimming duck was chosen as the subject for several reasons: the moving water system provided a readily controllable force against which the animal could work; surface swimmers had not previously been investigated; ducks are easily trained for the task; and the work cited above on flying birds provided data for an interesting comparison of similar animals engaged in dissimilar tasks.

### MATERIALS AND METHODS

#### *Animals*

Adult, male, mallard ducks (*Anas platyrhynchos*) with a mean body weight of 1081 g were used in this study. They were obtained from stock maintained at the Duke University Department of Zoology. All were less than 1 year old and none were

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moulting during the experiments. The ducks were kept in an outdoor pen with water sufficiently deep to allow free swimming.

### *Apparatus*

The ducks swam in an open, variable speed, water channel (Fig. 1). The channel of controlled flow (working section) was 1.20 m long, 0.45 m wide and 0.26 m deep. Water velocity was measured in the centre of the working section with a Prandtl-type pitot-static tube (United Sensor and Control Corp., model PDE 24 H22MW) and water manometers. The maximum error in this measurement arose from the reading of the manometers; it occurred at the slowest speeds and was no more than 2.5%. The depth for water velocity measurements (0.05 m) was chosen to approximate to the mean depth of the duck's hull.

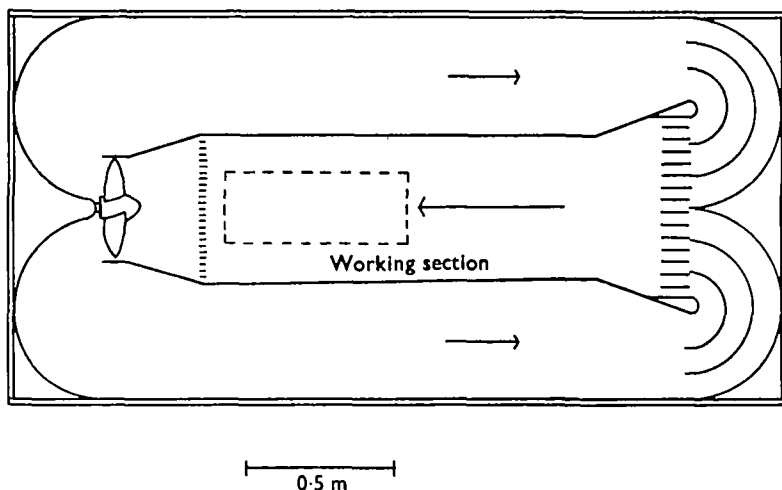


Fig. 1. Section of water channel. Direction of water flow is shown by arrows. Dashed line in working section indicates the location of the respiratory chamber where ducks swam during the experiments.

Turbulence, expressed as a percentage of the mean flow velocity measured with the pitot-static tube, was investigated in two ways. First, a dye stream was introduced at the front of the working section in the centre of the flow at a depth of 0.05 m. This stream had widened approximately 0.03 m from its centre when it reached the rear of the working section (measurement made at maximum water speed, 0.70 m/sec). This widening indicated movement normal to the mean flow velocity of 2.3%. Less turbulence was found at lower speeds.

The second method estimated turbulence as a variation in velocity parallel to the mean flow velocity. The static and total pressure outlets of the pitot-static tube were connected with  $\frac{1}{8}$  in (3.2 mm) I.D. Tygon tubing (1.4 m long) to a differential pressure transducer (Sanborn model 268 B). The output from the transducer was demodulated by a Sanborn model 321 carrier recorder. The monitor output from the recorder was alternately connected to a Heath Universal Digital Instrument (UDI) or a Root Mean Square (RMS) voltmeter (Ballantine, model 323-06). The mean flow velocity was calculated from 10 sec average values for dynamic pressure read from the UDI used

as a digital voltmeter. Since dynamic pressure varies as the square of velocity, the variation in velocity can be determined from the root mean square of the changes in dynamic pressure. The RMS voltage was therefore compared to the square root of the mean voltage from the UDI to calculate the percentage turbulence parallel to the mean flow velocity. Turbulence, as estimated with this method, was 13 %.

The minimum frequency of turbulence, determined from the carrier recorder chart, was approximately 25 Hz. From this frequency the maximum wavelength of the turbulence at a mean flow velocity of 0.70 m/sec can be calculated to be less than 0.03 m. The duck's hull is more than an order of magnitude greater than this wavelength. The variation in velocity measured with the pitot-static tube and turbulence were therefore considered unimportant to the experiments.

The ducks swam in a Plexiglass respiratory chamber 0.62 m long, 0.20 m wide, 0.20 m high at the front and 0.10 m high at the rear. These dimensions gave minimum chamber volume without interfering with the duck's swimming. Room air entered the chamber through holes at the rear and passed out through a manifold at the front. The chamber was suspended over the water surface of the working section. Flaps of thin rubber sheeting effected a seal between the lower edge and the water surface. Apparatus used to collect and analyse respiratory gases is discussed below with metabolic measurements.

#### *Training procedures*

A feeding tray and reward delivery system were attached to the front of the respiratory chamber. This system allowed the operator to deliver portions of about 2 g of granular food to the animal.

A duck, starved to approximately 90% of its *ad lib.* weight, was introduced to the chamber with the water still and food in the tray. When the animal discovered and ate the food the tray was refilled. When the duck learned to feed at the tray (usually after two or three trials) a slow flow of water was begun, forcing the duck to swim steadily as it fed. The ducks were trained in this way with gradually increasing water speeds for at least 2 weeks. As they learned to swim more steadily, the interval between rewards was increased and rewards were given only when the duck swam steadily at the front of the chamber.

The interval between rewards was varied from 15 to 90 sec to prevent entrainment to periodic rewards; the average interval was about 40 sec. The ducks usually required about 10 sec to eat the reward portion. They continued to swim steadily while eating their reward. If rewards were given as rapidly as the duck could eat them the oxygen consumption increased, but if rewards were given at intervals as described above there was no noticeable change in oxygen consumption. For this reason metabolic measurements were not interrupted when rewards were given.

The swimming speeds used for oxygen-consumption measurements ranged from 0.35 to 0.70 m/sec in 0.05 m/sec increments. This range was determined by the ducks' ability to sustain a given speed for the period required for measurement of steady-state oxygen consumption. At water speeds below 0.35 m/sec the ducks would not swim steadily; they swam to the front of the chamber, drifted back to the rear, and then repeated the cycle. At this low speed they appeared unable to swim with a regular stroke long enough to give satisfactory oxygen-consumption measurements.

The ducks were also unable to sustain swimming speeds in excess of 0.70 m/sec. At higher speeds they were washed back against the rear wall of the chamber and the experiment had to be terminated or the water velocity decreased to prevent possible injury to the animal.

Each duck swam every day throughout the course of the experiments. An irregular schedule of swimming speeds was set up so that no trend existed in the order of swimming speeds for a given duck and the entire range of test speeds was covered each day.

#### *Metabolic measurements*

The system used to collect and analyse respiratory gases is shown diagrammatically in Fig. 2. Two rotary vacuum pumps (Gast Mfg. Co., model 521) drew in the gases from the respiratory chamber through a 1 in (25 mm) I.D. hose at a flow rate of approximately 100 l/min. A 5 gal (18.7 l) container served as a mixing chamber and water trap. The flow rate was measured with a 12 l displacement flow meter (Vol-U-Meter, Brooks Inst. Div., Emerson Electronics) filled with dry air and connected to the system with a T valve. Flow-rate measurements were accurate to within 2%. A continuous sample (c. 0.2 l/min) was removed from the flow and pumped through a drying column (Drierite) into a Beckman G-2 paramagnetic recording oxygen analyser accurate to 0.001% oxygen. The overall accuracy of the system for measuring oxygen consumption was within  $\pm 3\%$ .

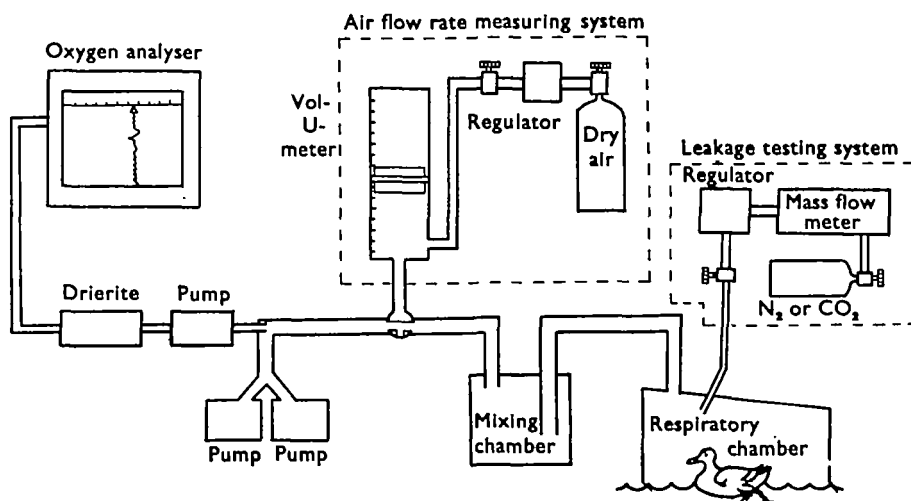


Fig. 2. Gas collecting and analysing system. Systems for measuring air flow and for testing for leakage are shown as connected when in use.

The system was tested for leakage as follows. A Matheson Mass Flowmeter (model no. 8110-0113) was calibrated with the aid of a Vol-U-Meter for use with pure nitrogen to an accuracy of 2%. A measured flow of nitrogen was infused into the empty chamber at the usual location of the ducks' head with the same air flow through the chamber as used in the actual experiments. The dilution of the air by the nitrogen reduced the partial pressure of the oxygen and was indicated by the oxygen analyser. The analyser reading was then compared to the value calculated from the known

flow rates for nitrogen and room air. This comparison showed there was no detectable loss of gas from the system.

The leakage-testing system was similarly employed to determine the possible loss of exhaled carbon dioxide to the water. The effect on the partial pressure of oxygen of infused carbon dioxide was compared to that of an equal infusion of nitrogen. The loss of carbon dioxide to the water was found not to be measurably different from that of nitrogen. All gas measurements were corrected to STPD.

For all experiments the air temperature was between 22 and 25 °C; the water temperature was between 22 and 24 °C. Wet and dry bulb thermometers placed in the air flow indicated a relative humidity of between 68 and 75 % over the range of water speeds used. Room air varied between 45 and 55 % relative humidity.

At the beginning of each experiment the air and water temperatures were recorded; air flow rate and oxygen analyser zero setting were checked; and the duck was weighed. The duck was then placed in the respiratory chamber and the water speed was set according to the daily schedule. Oxygen consumption was monitored until the indicated percentage oxygen varied less than 0.05 % for 10 min. (In longer experimental trials 10 min periods of steady oxygen consumption were found to be representative of the steady-state oxygen consumption.) After each experiment the duck was removed from the chamber and the air flow rate and oxygen analyser zero setting were re-checked.

The total time spent swimming during a successful run was usually about 20 min. If a steady oxygen consumption was not recorded in 20 min the run was terminated.

Resting oxygen consumption was determined in two ways: in still water in the respiratory chamber, and out of the water in a Plexiglass cylinder (0.38 m long, 0.16 m in diameter). The cylinder was open to room air at one end and connected to the mixing chamber at the other. In all other respects the analysing equipment was used as described for the oxygen-consumption measurements during swimming. The air and water temperatures were within the same ranges. The duck was left in either system with the room lights off or the chamber covered until the oxygen consumption reached a minimum steady-state level. The ducks usually appeared to go to sleep under these conditions.

### *Drag measurements*

Drag was measured by attaching a model duck to a Grass Instruments model FT-03 force transducer at various water velocities. A probe and lever system which responded to forces parallel to the water surface was attached to the transducer. One channel of a Sanborn model 321 carrier recorder provided the carrier signal for the force transducer and demodulated the output. The output from the recorder was averaged over 10 sec by a Heath Universal Digital Instrument operating as a digital voltmeter. These averages were recorded and used to determine drag force. The system was calibrated to an accuracy of  $\pm 4\%$  by suspending known weights from the probe. The mean of fifteen 10 sec readings was used to determine drag at each velocity.

The model used for drag measurements was based on a hunting decoy (Victor Decoy Co., model D-9). The decoy was modified to reproduce as nearly as practicable the hull shape and dimensions of a live duck. In addition the model was equipped with a vertical stabiliser to counteract a yawing tendency encountered at higher velocities. Attempts to measure drag on anaesthetized ducks or dead ducks frozen in

proper swimming postures were unsuccessful because of their instability at higher speeds.

*Measurement of stroke rate and free-swimming speed*

The stroke rate of paddling was measured on ducks swimming in the water channel during experimental runs. Strokes were counted and timed with a stopwatch.

Observations of ducks swimming freely on a large pond were made photographically. The speed of free-swimming ducks was calculated from the wave length of the first bow wave of the duck's wake. The ratio of the wave length to water-line length, as measured from photographs, was multiplied by the assumed water-line length of ducks (0.33 m measured on experimental animals) to give the wave length. Velocity of a wave, and hence that of the duck, can be calculated from the formula

$$V = (gL/2\pi)^{\frac{1}{2}},$$

where  $V$  is velocity, m/sec;  $g$  is gravitational acceleration, 9.8 m/sec<sup>2</sup>; and  $L$  is wave length, m. Only ducks engaged in steady swimming were selected for these observations.

## RESULTS AND DISCUSSION

### *Metabolic studies*

The mean resting oxygen consumption of ducks sitting still in the water beneath the respiratory chamber was 1.28 l/kg.h (Fig. 3). The mean value obtained from ducks in the dry chamber was 0.93 l/kg.h. The ducks in the water were less restrained than those in the dry chamber, and the higher oxygen consumption may have resulted either from their movements in the respiratory chamber or from compensation for heat loss to the water. Because of these extra contributions to resting level the dry-chamber measurement was considered to represent more accurately the resting oxygen consumption of the duck.

Pickwell (1968) gives values for resting rates of mallard ducks of 67–120 kcal/kg.min which may be converted to an oxygen consumption of 0.89–1.50 l/kg.h. Calculations from the relationship between body weight and metabolic rate for non-passerine birds given by Lasiewski & Dawson (1967) predict a mean resting oxygen consumption of 0.67 l/kg.h. Because these values from the literature differ so greatly the value measured in this study will be used where a value for resting oxygen consumption is required.

The oxygen consumption of the swimming ducks is about twice the resting level at speed from 0.35 to 0.50 m/sec (Fig. 3). From 0.55 m/sec the oxygen consumption increased rapidly to more than four times the resting level at the highest sustained swimming speed (0.70 m/sec).

Because of the influence of body size on metabolic rate the comparison of the maximum metabolic capability of the swimming duck with that of other animals may best be made in terms of multiples of the resting metabolic rate. Hemmingsen (1960) collected reports of maximum sustained work and found the maximum level of metabolic rate proportional to the same power of body weight as the resting rate, but about 20 times greater. More recent studies, however, give lower multiples. Lasiewski (1963)

gives a maximum sustained metabolic rate for a hovering hummingbird of 15.4 times resting. LeFebvre's data (1964) gives a multiple of 13.4 for a pigeon in flight. Tucker's (1968) study on the flying budgerigar indicates a multiple of 12.8. By comparison the maximum sustained metabolic rate for the swimming duck of only 4.1 times resting seems rather small.

An explanation for the lower maximum found for the swimming duck may be sought from an examination of the muscle masses involved in the locomotion. The maxima attained by the other birds in flight presumably are proportional to the activity of the flight muscles. If the maximum metabolic rate of a duck during sustained swimming is proportional to the activity of the leg (swimming) muscle mass then the maximum sustained metabolic rate for a flying duck may be proportional to the muscle mass used for flight.

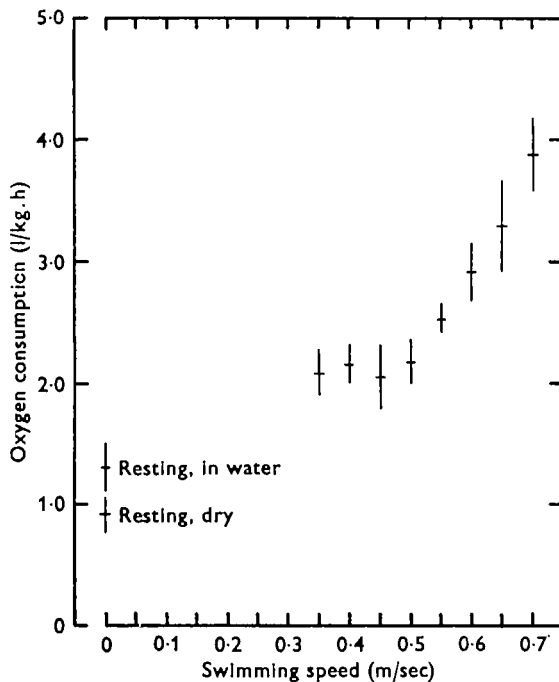


Fig. 3. Mean oxygen consumption (horizontal lines) of four ducks at different swimming speeds. Vertical lines represent two standard errors on either side of the mean.

The flight muscles dissected from one of the ducks used in this study weighed 200 g. The muscles of both legs weighed 72 g. The ratio of flight muscle weight to swimming muscle weight is 2.3:1. The product of the maximum swimming metabolic rate and this ratio gives 11.6 times resting as the estimated maximum sustained metabolic rate for the flying duck. This estimate agrees well with the maximum sustained metabolic rates for flight found for other flying birds.

The agreement between this estimated maximum of flying metabolic rate and those measured for other birds in flight suggests that the lower maximum sustained rate found for the swimming duck may be a function of the smaller muscle mass used for swimming. The ducks were never observed to show any evidence of fatigue even after

as much as an hour of steady swimming at the highest speeds observed. From these observations it seemed that respiratory function did not limit the maximum swimming speed.

A possible explanation for the limit of maximum sustained swimming speed for the duck may be found from an investigation of the water resistance (drag) to the movement of surface ships through the water. Studies on ships and ship-hull models (see, for example, Taylor, 1933) indicate that, as a ship nears its maximum speed, the energy dissipated into wave making is the largest component of drag on the hull. The maximum practical speed for conventional displacement hulls has been found to be a function of an interaction between the length of the hull and the wave length of the wave systems, propagated at the bow and stern of the hull, which make up the wake. The wave length of waves ( $L$ ,  $m$ ) is related to the speed at which it moves along the water surface ( $V$ ,  $m/sec$ ) by the relationship  $L = 2V^2/g$ , where  $g$  is gravitational acceleration,  $9.8\text{ m/sec}^2$ .

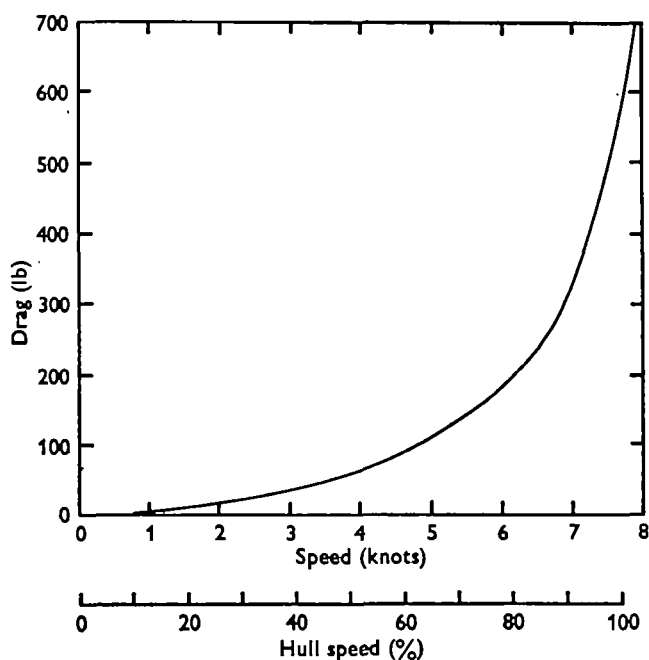


Fig. 4. Drag on a 32 ft (9.6 m) ship hull plotted against actual speed and percentage hull speed. Figure adapted from Marchaj (1964).

When the hull reaches the speed where the wave length of the bow wave equals the water-line length of the hull (hull speed) the bow wave constructively interferes with the stern wave and the hull becomes 'trapped' in the trough between the bow and stern waves. As a result, as hull speed is approached, resistance to further increase in speed increases nearly asymptotically. An example showing the rapid increase in drag on a ship hull as hull speed is approached is shown in Fig. 4. The relationship of oxygen consumption to swimming speed (Fig. 3) for the swimming duck is similar in its rapid increase as the maximum swimming speed sustainable by the ducks is approached.



The mallard ducks used in this study had a water-line length of 0.33 m. From this length a hull speed of 0.71 m/sec can be calculated. The agreement between this hull speed and the observed maximum sustained swimming speed of the ducks used in this study (0.70 m/sec) together with the rapid increase in oxygen consumption as hull speed is approached implies that the swimming speed of the ducks is subject to constraints similar to those found in ships with conventional displacement hulls.

It should be noted that, for short bursts, the ducks were able to swim in excess of their theoretical hull speed. This higher speed performance apparently could not be maintained for more than a few seconds. Furthermore, except for brief periods when they are moulting, it seems unlikely that ducks would call upon swimming for a means of rapid movement or escape when flight is available to them as an alternative.

#### Cost of transport

Although the rate of utilization of fuel is of interest when comparing metabolic processes, it may be of less importance to the animals than the total fuel consumed in travelling from one point to another. An animal might, for example, minimize the cost of transporting itself by using fuel at a high rate while covering a distance in a shorter time. Thus the cost of transport (ratio of metabolic rate to speed of travel) reflects directly the amount of fuel the animal uses to cover a given distance.

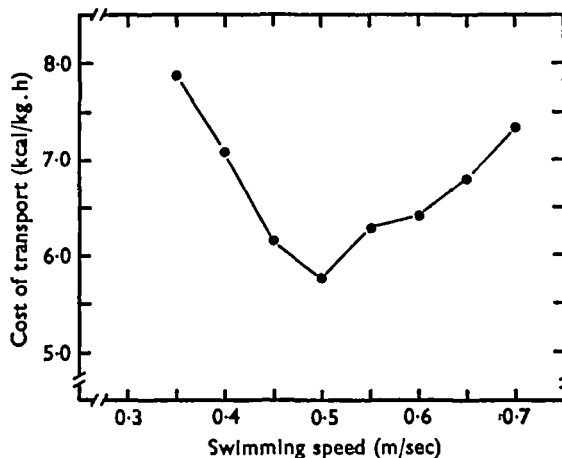


Fig. 5. Mean cost of transport of four ducks at different swimming speeds.

When the cost of transport for the ducks is compared to the swimming speed (Fig. 5) the minimum value gives the speed at which the duck can most economically travel a given distance. In this study the minimum cost of transport (5.77 kcal/kg.km) was found at a swimming speed of 0.50 m/sec.

This experimentally derived speed for minimum cost of transport was compared to the speed of mallard ducks observed swimming freely across a large pond. Photographs of the wakes of the free swimming ducks were analysed to determine the speed naturally chosen by ducks to swim across the pond. The speed calculated from these wave-length measurements indicated that the observed ducks swam freely with a mean speed of 0.48 m/sec (range 0.45–0.51 m/sec). Within the accuracy of the method this

mean value is indistinguishable from the experimentally derived value of 0.50 m/sec for minimum cost of transport. Ducks free to choose their speed when swimming unhurriedly seem to prefer the speed which gives minimum cost of transport.

### *Drag and efficiency*

Drag measurements were made on a model duck to compare with similar measurements on ships and to estimate the overall efficiency (power output/power input) of the swimming duck. The rapid increase in drag as hull speed is approached for the model duck (Fig. 6) is similar to that seen for the much larger ship (Fig. 4). This similarity suggests that the same hydrodynamic constraints operate on the duck as on the ship.

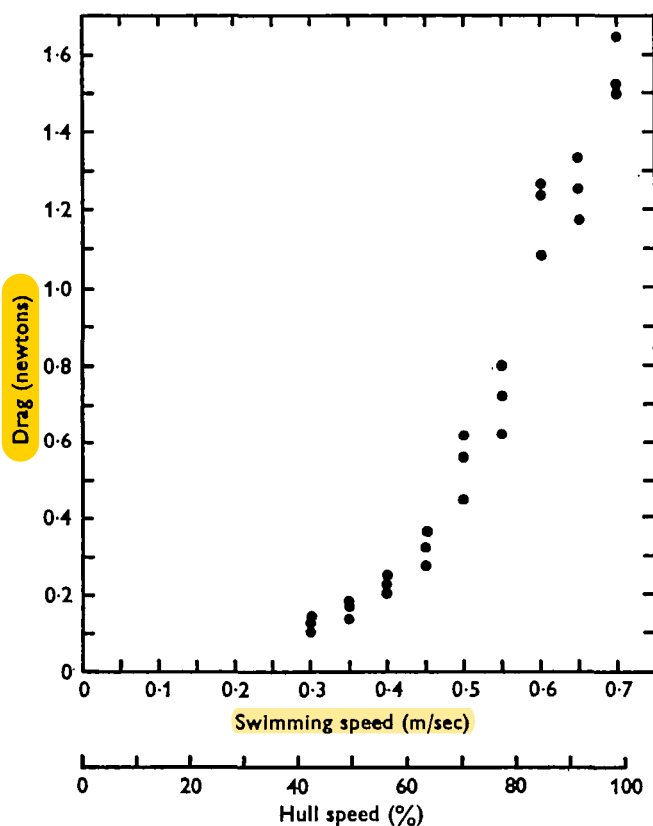


Fig. 6. Drag on a 0.33 m model duck plotted against actual speed and percentage hull speed. Each point is the mean of five measurements.

One of the parameters necessary for the calculation of efficiency of a system is the power output. If the estimate of power output for the swimming duck is to be meaningful, the assumption that the drag measurements obtained from the model are valid for a live duck must be well founded. Wave making is the largest component of drag on a displacement hull as it nears its maximum speed or hull speed. The characteristics of the model which affect wave making, hull length, shape and displacement were therefore matched closely to those features of live ducks.

The model differed from a live duck in two ways; the drag of the legs during the return stroke could not be duplicated on the model, and the rigidity and texture of the model hull were dissimilar to those of a live duck. Because of their relatively small area the contribution of the legs to the total drag is probably small. The drag of the model's vertical stabilizer, attached to counteract yaw at higher towing speeds, was considered partially compensatory for the drag normally created by the return stroke of the leg.

The surface irregularities of the model and of live ducks were of similar magnitude (2–4 mm) although the pattern of irregularities differed. The profile of the live duck's hull was never observed to be deformed during swimming. The model with its more rigid hull was therefore considered to give a reasonable approximation of the drag on live ducks swimming in the water channel. Ducks swimming on a still pond or slow river probably encounter essentially laminar flow. The flow in a water channel at the dimensions and speed used is necessarily somewhat turbulent and may have affected the drag on the duck's hull.

The efficiency of an active animal system may be variously described depending on the level of analysis and the definition of power input. Because the power output could only be estimated in terms of the whole animal, the measurement of metabolic rate for the whole animal was preferred as a value for power input.

The power input may be further considered as either the total metabolic rate during activity, or the difference between the total active metabolic rate and the resting or maintenance rate. The latter case is intended to consider only the cost of the activity. However, the necessary assumption that energetic requirements for maintenance remain constant during elevated metabolic activity is difficult to substantiate; also there is no basis from which to assume a resting or maintenance 'metabolic rate' for the ships with which the duck is compared; and the total energy input seems more relevant biologically to the demand for fuel from the environment. For these reasons the total metabolic rate has been used for the definition of power input in these efficiency calculations.

Efficiency calculated from total power input has been termed 'gross' or 'overall' efficiency (Brody, 1964) or 'total' efficiency (Kleiber, 1961). Efficiency for the ship was calculated from the ratio of effective horsepower (rate of work done in moving the ship) to the power input calculated from fuel consumption. All efficiencies are expressed as percentages.

The drag at different velocities was used to estimate power output of the swimming duck. The product of the drag force (newtons) and the velocity (m/sec) gives the power output ( $\text{N} \cdot \text{m}/\text{sec} = \text{W}$ ). The power input can be calculated from the steady-state oxygen consumption. If the respiratory quotient is 0.8 the caloric equivalent of 1 l of oxygen is 4.8 kcal. Since 1 kcal equals 1.16 Wh, an oxygen consumption of 1 l/h reflects a power input of 5.57 W. The data for the ducks' mean drag, oxygen consumption, power output, power input and efficiency at the swimming speeds studied are given in Table 1.

The overall efficiency increased with increasing swimming speed and reached a maximum of 4.7% at the maximum speed. The maximum overall efficiency for the duck is less than that found for ships (c. 22%, according to calculations based on data from Hughes, 1942).

The maximum overall efficiencies calculated for terrestrial animals (man, horse dog) are typically in the range of from 20 to 30 % (Brody, 1964). These efficiencies are reached with the subjects pulling loads or climbing grades. Perhaps a more appropriate comparison might be made between the efficiency of a terrestrial animal running unburdened on a level surface and that of the swimming duck. For the swimming duck the power output values are based on the drag of the water on the duck's hull. In the corresponding case for the terrestrial animal the power output would be based on the air resistance of its body.

For a running man, if his shape is assumed to be cylindrical, the air drag can be calculated to be about 7.7 N at 4 m/sec, an appropriate speed for a distance runner. The power output at that speed is then 30.8 W. Oxygen consumption at that speed is about 4 l/min (Webb, 1964) which represents a power input of 1340 W. The overall efficiency for running calculated from these data is therefore 2.3 %. It is apparent therefore, that neither the duck nor the runner dissipates much of the total power input to fluid resistance.

Table 1. *Efficiency of swimming*

Swimming speed (m/sec)	Mean drag (newtons)	Mean oxygen consumption (l/h)	Power output (watts)	Power input (watts)	Overall efficiency (%)
0.35	0.156	2.24	0.055	12.48	0.04
0.40	0.225	2.32	0.090	12.92	0.7
0.45	0.318	2.21	0.143	12.31	1.2
0.50	0.634	2.34	0.317	13.03	2.4
0.55	0.716	2.82	0.394	15.71	2.5
0.60	1.17	3.15	0.703	17.55	4.0
0.65	1.18	3.55	0.770	19.77	3.9
0.70	1.56	4.18	1.09	23.38	4.7

A ship increases its speed by increasing the rate at which the propeller or paddle wheel turns. The duck, however, was observed to paddle at a constant stroke rate at all swimming speeds (Fig. 7). Since the web of the duck's foot appeared to be fully opened at all speeds, increases in swimming speed were probably accomplished by an increase in length of the path followed by the foot.

The observation of a constant stroke rate raises the possibility that the duck's leg may oscillate at a resonant frequency and use the elastic components of the leg for restoring force.

#### *Concluding discussion*

None of the other swimmers, men and fish, for which metabolic data are available, are directly comparable to ducks. Fish are not subject to the hydrodynamic constraints of wave making; on the other hand they are limited by environmental temperature and availability of oxygen (Brett, 1964, 1967; Fry & Hart, 1947). Under best conditions young salmon can increase their metabolic rate to 12.7 times resting (Brett, 1967). Men are awkward swimmers at best and therefore cannot really be compared meaningfully to other swimming animals in terms of swimming performance. Human swimmers increase their metabolic rate to 10–12 times resting at a steady

swimming speed of 0.7 m/sec (Andersen, 1960). This level is similar to the metabolic rate for a man running at 3.3 m/sec (Webb, 1964). The maximum multiples of sustained swimming metabolic rate for both men and fish are greater than that for the duck which was 4.1 times resting.

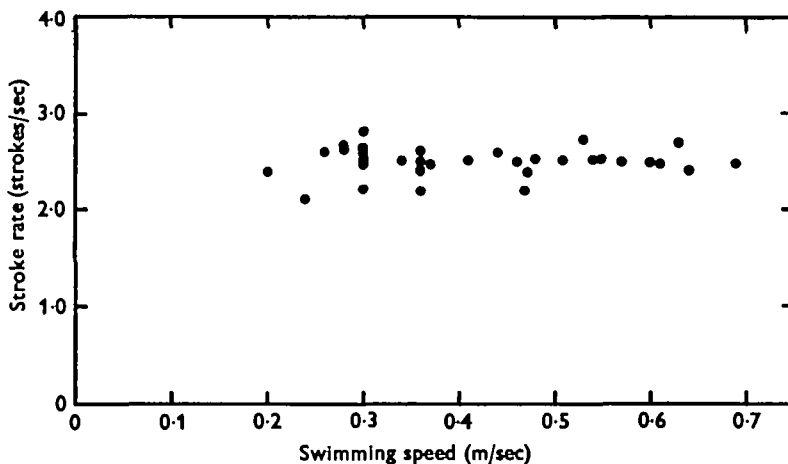


Fig. 7. Stroke rate of duck's feet at various swimming speeds. A linear least squares regression line for the data has the equation: Strokes/sec =  $2.44 + (1.14 \times 10^{-6} \times \text{swimming speed, m/sec})$ .

The minimum cost of transport for the swimming duck (5.77 kcal/kg.km) is about seven times greater than the estimated cost of transport for a flying bird of the same weight (0.8 kcal/kg.km, Tucker, 1970). The minimum cost of transport for a ship is more than 200 times less than that for a swimming duck. On a basis of relative weight, the ships' cost of transport is lower than Tucker's equations would predict for any animal. The cost of transport for a salmon is much less than that of walkers or flyers of comparable body weight. The cost of transport for a human swimmer (35.4 kcal/kg km) is six times greater than that for a swimming duck and 30 times greater than that for a running man.

The duck's drag-velocity relationship resembles that for a ship although the duck has a much lower overall efficiency for overcoming its drag. Human swimmers, in measurements of pull against a spring dynamometer, indicated maximum efficiencies up to 2.2% (Karpovich, 1966), slightly less than the ducks' calculated efficiency. The human subjects were, however, held stationary while swimming, and the flow of water around the swimmer was therefore dissimilar to that around a swimmer propelling himself through the water.

That the swimming duck is less efficient than the ship may be an irrelevant comparison. The difficulty of defining the physical work done within the animal in terms of discrete functions has necessitated the use of the parameter overall efficiency. Many of the functions which must be continued while the duck swims may not be directly involved in the locomotion and may have no counterpart in the ship. These activities increase the total energy input in excess of that which is required for propulsion through the water. Thus the efficiency of swimming as described may be lower than that of a ship only because the cost of maintaining a living system cannot

be separated from the locomotive costs. The parameter, efficiency, is therefore of little use in comparing animal systems with machinery unless the animal processes can be more strictly defined and measured.

There is, however, an hydrodynamic parameter which may provide a more valid comparison of the ship and the duck. The theoretical maximum speed of a conventional displacement-hulled ship, its hull speed, is a function of the square root of its water-line hull length, as described above. For this reason the maximum speed of a hull is frequently described in terms of the speed/length ratio,  $V/(L)^{1/2}$ . When the speed is expressed in knots and the hull length in feet, this ratio has its practical limit at hull speed or a value of 1.35. In actual practice the speed/length ratio seldom exceeds unity for conventional ships.

The mallard's hull length (0.33 m) is about 1.1 ft; its maximum swimming speed (0.70 m/sec) is about 1.4 knots. The speed/length ratio for the duck is therefore about 1.34. On the basis of this parameter the duck's swimming performance excels that of most ships.

Furthermore, if one assumes that the mallard, like other birds in flight, could sustain metabolic rates of eight to twelve times resting, the achievement of nearly the theoretical speed limit for its hull length while elevating its metabolic rate to only 4.1 times resting must also be considered an index of excellent performance. Presumably the ship is utilizing the maximum output of its power plant to attain its maximum speed while the duck may be employing as little as one-third of its potential maximum output to accomplish a similar feat.

It should also be considered that the requirements of swimming are only one part of the many factors which affect the evolution of the duck. The duck's legs must also serve for locomotion on land. Furthermore, the weight of the propulsive system must also be limited by the requirements of low weight for flight. Despite these apparent limitations the duck is able to swim at the theoretical speed limit for its hull and, in doing so, expend energy at a rate well below its estimated maximum metabolic capability.

#### SUMMARY

1. The metabolic cost of swimming was studied in mallard ducks (*Anas platyrhynchos*) which had been trained to swim steadily in a variable-speed water channel.

2. At speeds of from 0.35 to 0.50 m/sec the oxygen consumption remained relatively constant at approximately 2.2 times the resting level. At speeds of 0.55 m/sec and higher the oxygen consumption increased rapidly and reached 4.1 times resting at the maximum sustainable speed of 0.70 m/sec.

3. The maximum sustainable swimming speed of the ducks coincided with the limit predicted from hydrodynamic considerations of the water resistance of a displacement-hulled ship of the same hull length as a duck (0.33 m).

4. The cost of transport (metabolic rate/speed) reached a minimum of 5.77 kcal/kg km at a swimming speed of 0.50 m/sec. Ducks swimming freely on a pond were observed to swim at the speed calculated in experimental trials to give minimum cost of transport.

5. Drag measurements made with model ducks indicated a maximum overall efficiency (power output/power input) for the swimming ducks of about 5%. Ships

typically have maximum efficiencies of 20–30%. Because of the difficulty in delimiting the cost of swimming activity alone from the other bodily functions of the duck, overall efficiency may present an incorrect description of the swimming performance of the duck relative to that of a ship. An hydrodynamic parameter such as speed/length ratio [speed/(hull length)<sup>4</sup>] whereby a duck excels conventional ships may present a more appropriate comparison.

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