

HYDROPLANING BY DUCKLINGS: OVERCOMING LIMITATIONS TO SWIMMING AT THE WATER SURFACE

TERRY L. AIGELDINGER AND FRANK E. FISH*

Department of Biology, West Chester University, West Chester, PA 19383, USA

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Summary

Rapid escape behavior by mallard (*Anas platyrhynchos*) ducklings is restricted to burst swimming at the water surface. Maximum speed may be limited because of the pattern of waves created as the duckling's body moves through the water (hull speed). Burst speeds for 9-day-old ducklings were compared with predicted hull speeds, based on the waterline length of ducklings either resting in water or actively swimming. Kinematic analysis of video tapes showed a mean maximum burst speed of 1.73 m s^{-1} , which was four times greater than the predicted hull speed. At burst velocities, stroke frequency was 1.9 times higher than

the stroke frequency measured during steady low-speed paddling. Transition to burst speeds from steady paddling occurred near predicted hull speed. The paddling motions of the webbed feet were used to generate both thrust and lift. By using lift to raise the body above the water surface, the influence of waves in restricting maximum swimming speed is negated. The duckling's body becomes a planing type of hull and skims on the water surface.

Key words: hydroplaning, ducklings, wave drag, swimming kinematics, mallard, *Anas platyrhynchos*.

Introduction

To survive, designated prey can fight, hide or flee (Weihs and Webb, 1983; Feder and Lauder, 1986). To flee in open water, adult mallard ducks (*Anas platyrhynchos*) are capable of using a variety of methods to escape predation. Ducks can fly above or dive under the water surface, or they can swim away at high speeds on the surface of the water. However, young ducklings are developmentally constrained from using some of these escape tactics. Flight capability of ducklings is not achieved until 49–60 days (Bellrose, 1976). Diving is energetically expensive because a duck spends most of its power to overcome buoyancy (Butler and Woakes, 1984; Stephenson *et al.* 1989; Wilson *et al.* 1992; Lovvorn *et al.* 1991; Stephenson, 1994). In addition, small animals have short dive durations (Kooyman, 1989), making diving a poor method of escape for ducklings. The only method of escape remaining for a duckling is high-speed swimming at the water surface.

Relatively few animals swim at the water surface for extended periods (Vogel, 1988). Indeed, many aquatic vertebrates avoid the surface by swimming at depth or leap clear of the water to travel through the air. These strategies may reduce the energy required for locomotion (Au and Weihs, 1980; Blake, 1983; Hui, 1987; Williams, 1987, 1989) and avoid predation (Moore, 1955; Fish, 1990; Webb *et al.* 1991).

Speed at the water surface is constrained by the formation of surface waves. As an animal swims at the surface, it pushes water out of the way, as do ships with conventional

displacement hulls (Prange and Schmidt-Nielsen, 1970). The flow around a displacement hull generates transverse waves at the bow and stern. The waves result from pressure variation due to differential water velocities around the hull (Marchaj, 1964; Kay, 1971; Sorensen, 1973; Foley and Soedel, 1981). The number of waves varies directly with hull length and velocity. As velocity increases, the wavelength of the system increases until the wavelength of the bow wave matches the hull length (Foley and Soedel, 1981). Bow and stern waves increase in amplitude as the waves come into phase and constructively interfere (Marchaj, 1964; Kay, 1971; Sorensen, 1973). The hull becomes trapped in a wave trough of low pressure situated amidships. The bow wave, with increased size and inertia, cannot flow out of the way quickly enough to allow an increase in the velocity of the hull (Kay, 1971). This effective speed limit is called the hull speed. Wave drag results from the increased work required to climb up the bow wave and from the transfer of kinetic energy from the moving hull to the water. Wave drag increases steeply and becomes the dominant drag component as hull speed approaches (Hertel, 1966; Sorensen, 1973).

For animals swimming at the water surface at their hull speed, constructive interference from bow and stern waves traps the animal in a trough, ultimately limiting further increases in speed (Vogel, 1988; Denny, 1993). To move faster, the animal would literally have to swim uphill, which

*Author for correspondence.

is energetically very costly (Prange and Schmidt-Nielsen, 1970). Adult ducks (Prange and Schmidt-Nielsen, 1970), muskrats (Fish, 1982), mink (Williams, 1983) and sea otters (Williams, 1989) at the surface rarely exceed hull speed. Data from Kolmogorov and Duplishcheva (1992) and Videler (1993) show that competitive human swimmers reach hull speed at their maximum swimming speeds. Videler (1993) suggests that future record speeds would come from longer swimmers and thus higher hull speeds.

Prange and Schmidt-Nielsen (1970) found agreement between hull speed and maximum sustained speed for adult mallard ducks. As hull speed was approached, the drag and oxygen consumption of the duck increased rapidly. Hull speed was calculated as 0.71 m s^{-1} for an adult duck with a waterline length of 0.33 m. The small size of ducklings implies a lower hull speed, because hull speed depends on the waterline length of the body, with longer bodies having higher hull speeds. This study investigates whether ducklings are limited by hull speed during burst swimming.

Materials and methods

Animals

Sixteen mallard ducklings (*Anas platyrhynchos* L.) were obtained from a commercial dealer approximately 24 h after hatching. Ducklings were housed individually in $0.27 \text{ m} \times 0.53 \text{ m} \times 0.38 \text{ m}$ cages. Animals were maintained on a light cycle of 12h:12h L:D at ambient temperatures of 20–25 °C. An infrared heat lamp was provided during the first week. A diet of starter duck feed (Purina) and water were supplied *ad libitum*. Ducklings were exercised daily by swimming for 15–20 min at 0.3 m s^{-1} in a recirculating water channel (Fish, 1994).

Apparatus

Experiments were conducted on 9-day-old ducklings in a 380 l rectangular glass aquarium ($1.85 \text{ m} \times 0.50 \text{ m} \times 0.48 \text{ m}$) filled with water (26 °C) to a level of 0.27 m. A divider that did not pierce the water surface was placed lengthwise in the unfilled portion (i.e. above the water) of the aquarium. The divider forced the ducklings to swim in a straight path in a narrow (0.14 m) trackway on the water surface. Vertical reference lines, 0.2 m apart, were painted on the divider.

Ducklings were videotaped at 60 Hz with a Panasonic video cassette recorder AG-7300 and Panasonic system camera (WV-D5100) equipped with a Panasonic (WV-LZ14/12) 12× zoom lens (1:1.6, 10.5–126 mm). A time-code signal was recorded on the video tape with a Horita TRG-50 SMPTE time-code generator. The camera was perpendicular to, and approximately 2 m from, the long axis of the aquarium; its viewing field was limited to a 0.39 m wide region in the center of the trackway. A 0.10 m scale placed in the trackway at a depth of 0.06 m was videotaped and then removed prior to experimental trials. Two 500 W floodlamps were positioned in front of the aquarium.

Images of ducklings swimming along the trackway were

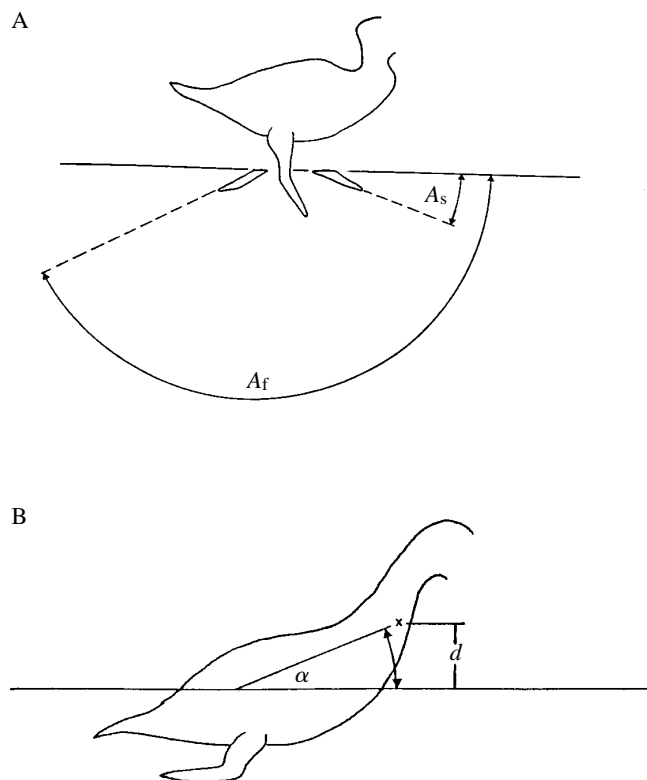


Fig. 1. (A) Angles measured between the horizontal plane and the longitudinal axis of a paddling foot. A_s is the angle at the start of the power phase of the stroke cycle, A_f is the angle at the end, and the arc angle A_a is $A_f - A_s$. (B) Angle of trim α and vertical displacement d measured on a burst swimming duckling. The cross indicates the position of a marker placed on the breast of the duckling. The marker was at the level of the water surface when the duckling was at rest.

digitized from individual fields of video tape with an AT-compatible computer, Panasonic AG-7300 video recorder, Sony PVM 1341 monitor and Peak Performance Technologies video analysis system (Peak 2D, version 4.2.4). Measurements were made of horizontal and vertical displacements, velocity, waterline length of the body, stroke frequency, angles of feet with respect to the horizontal and angle of trim. Foot angles were measured at the beginning, A_s , and end, A_f , of the power phase (Fish, 1984) of the stroke cycle (Fig. 1A). The difference between A_s and A_f was the arc angle A_a , representing the angular displacement of a foot over the stroke. Angle of trim (Saunders, 1957; Hammitt, 1975) was the angle between the longitudinal axis of the body and the horizontal plane (Fig. 1B).

Experimental trials

A reference point was painted on the breast of each duckling with a white, non-toxic liquid marker (Liquid Paper, Gillette Co.) before each trial. The reference point was placed on the waterline level of the motionless, floating body. This point permitted measurement of vertical displacement of the body due to swimming motions (Fig. 1B). An individual duckling was videotaped initially for 1 min as it swam undisturbed in

the trackway. Thereafter, burst swimming was induced by a startle reaction from a loud noise or gentle prodding. Burst swimming from one end of the trackway to the other was continued for 2 min or until the duckling would burst swim no longer. After a 30 min rest, swimming trials were repeated twice more. Only those video sequences in which ducklings swam steadily (i.e. without apparent accelerations or decelerations of the body) in a straight line without contact with the walls of the aquarium were used.

Swimming velocity and hull speed

Average velocity, U , was calculated as the horizontal distance traversed in a swimming sequence divided by the elapsed time. Average velocity was determined from sequences in which ducklings swam steadily.

The theoretical maximum speed of a conventional displacement hull, such as a ship or duck, is hull speed, U_h (Prange and Schmidt-Nielsen, 1970). Hull speed in deep water is a function of the square root of the waterline length of the hull or body:

$$U_h = (gl_w/2\pi)^{1/2}, \quad (1)$$

where g is the gravitational acceleration, 9.8 m s^{-2} , and l_w is the waterline length along the longitudinal axis of the body (in m). As a result of possible changes in the conformation of the body with swimming style, maximum hull speed was calculated separately for paddling, U_{hp} , and bursts, U_{hb} .

To adjust for differences in speed due to size, the dimensionless Froude number F was computed:

$$F = U/(gl_w)^{1/2}. \quad (2)$$

The Froude number represents the ratio of inertial forces to gravitational forces experienced by a body moving at or close to a fluid/fluid interface (Webb, 1975). Hull speed is reached at a Froude number of 0.40 (Vogel, 1988).

Differences between routine paddling and burst swimming for the kinematic variables were subjected to a t -test. Variation about means is expressed as \pm one standard error (S.E.M.).

Results

Swimming velocity and hull speed

A total of 277 swimming sequences were recorded, of which 184 sequences were acceptable for analysis, including 43 paddling and 141 burst swimming sequences. Theoretical hull speeds, calculated from equation 1, for paddling (U_{hp}) and burst swimming (U_{hb}) were 0.43 m s^{-1} and 0.47 m s^{-1} , respectively. U_{hb} was significantly greater than U_{hp} ($P < 0.05$). The higher value of U_{hb} was due to a 19.3% increase in the waterline length for burst swimming ($0.14 \pm 0.01 \text{ m}$) versus paddling ($0.12 \pm 0.01 \text{ m}$) ducklings. Mean paddling U ($0.33 \pm 0.02 \text{ m s}^{-1}$) was significantly lower than U_{hp} by 23.3% ($P < 0.001$), although the range of paddling U was 0.10 – 0.55 m s^{-1} .

The difference between theoretical and measured burst velocities was significant ($P < 0.001$). Mean burst speed ($1.26 \pm 0.02 \text{ m s}^{-1}$) was 2.7-fold greater than U_{hb} , representing

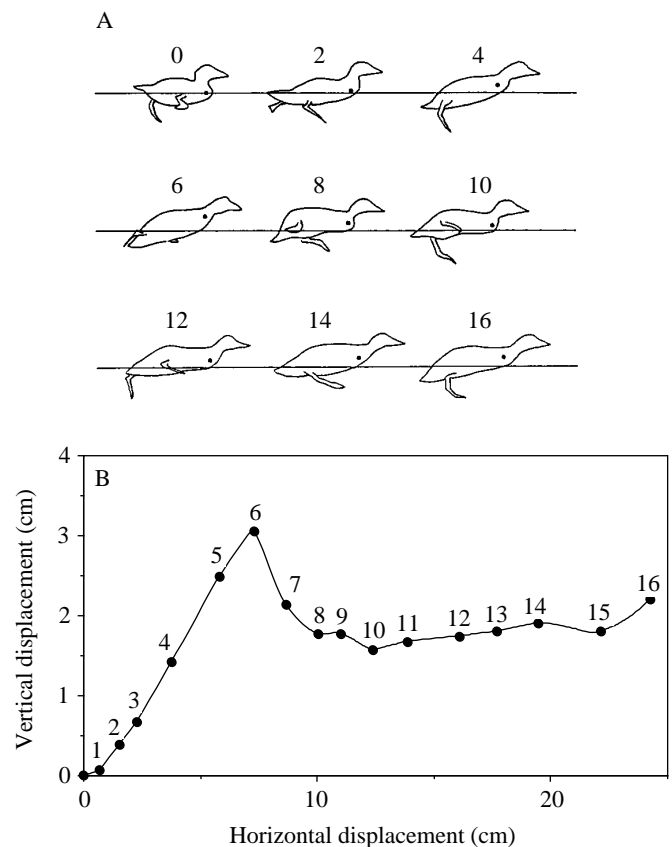


Fig. 2. (A) Sequence of tracings for a swimming duckling showing the transition from paddling to burst swimming. Numbers indicate fields from the video tape (0.017 s between fields). The horizontal line represents the water level at rest. The solid dot on each tracing shows the position of the marker placed on the duckling's breast. Fields 0–2 show the duckling steadily paddling using alternate strokes of the feet. Fields 4–6 show the initiation of burst swimming. The duckling moves forwards and upwards. With a positive angle of trim, the duckling uses alternate paddling as it burst swims (fields 8–16). (B) Vertical and horizontal displacements of the duckling shown in A. Numbers indicate fields of video tape. Large displacements occur at the initiation of burst swimming (fields 3–6). After the duckling has jumped over its bow wave, the animal proceeds with its body elevated above the water surface (fields 7–16).

a relative swimming speed of 3.9 body lengths s^{-1} . With an average U of 1.53 m s^{-1} , one duckling had a peak instantaneous velocity of 2.54 m s^{-1} (18.5 body lengths s^{-1}).

The F ranges for paddling, 0.10 – 0.49 , and for burst swimming, 0.46 – 1.50 , overlapped. Only maximum values of F for paddling exceeded those predicted at hull speed ($F = 0.40$), whereas for burst swimming, F was always above the theoretical limit.

Displacement and trim angle

Conformational changes in the body were noted between paddling and burst swimming (Fig. 2A). During paddling, the marker on a duckling's breast remained near the waterline (Fig. 2A). In addition, the longitudinal axis of the body was parallel

to the water surface with the neck held perpendicularly. By contrast, burst swimming ducklings raised the anterior portion of their bodies out of the water by 0.02 ± 0.01 m (Fig. 2A,B), resulting in a trim angle of $15.6 \pm 0.49^\circ$. Trim angle for burst swimming ducklings was significantly different from zero ($P < 0.001$).

Swimming kinematics

Paddling by ducklings was characterized by alternate power and recovery sweeps of the hindfeet (Fig. 2A; fields 0–2) as in other semiaquatic paddlers (Fish, 1984). During the power phase, the foot was swept posteriorly through an arc with the interdigital webbing fully spread (abducted). The foot was plantarflexed at the tibiotarsus–tarsometatarsus joint and the digits were dorsiflexed. During the recovery phase, the foot was swept anteriorly as the foot was dorsiflexed. The webbing of the foot was collapsed by adduction and plantarflexion of the digits.

Burst swimming was initiated by a rapid simultaneous sweep of the feet or by a large excursion of a single foot (Fig. 2A; fields 4–6). This motion effected an increase in the horizontal and vertical displacements of the duckling (Fig. 2B). Vertical displacement peaked at the end of the power phase. In instances in which a burst was initiated in the center of the viewing field, the duckling was observed to leap over its own bow wave. Subsequent forward progression was produced by alternate paddling motions. The marker on the duckling's breast remained above the water surface for the duration of the burst swimming bout.

A_s was not significantly different between paddling and burst swimming, with mean values of $18.16 \pm 1.26^\circ$ and $17.49 \pm 0.59^\circ$, respectively. Conversely, A_f during burst swimming ($146.78 \pm 0.77^\circ$) was 51% greater ($P < 0.05$) than during paddling ($97.02 \pm 2.77^\circ$) and accounted for the significant ($P < 0.05$) 64% increase in burst A_a . During paddling, A_a increased linearly with increasing U (Fig. 3A; mean $78.86 \pm 2.16^\circ$), while A_a remained constant ($129.29 \pm 0.83^\circ$) over the range of burst swimming speeds.

Stroke frequency remained constant at 3.78 ± 0.09 Hz for paddling and at 7.12 ± 0.08 Hz for burst swimming (Fig. 3B). Frequency changed abruptly near the theoretical hull speed of the ducklings.

The low A_s and rapid movement of the feet during burst swimming ventilated air from the surface (Fig. 4). The air was transported as bubbles with the foot through the power phase. At the end of the power phase, the bubbles in the wake continued to move downwards and backwards in the form of a vortex ring. Thus, the alternate and periodic motion of the feet left a trail of regularly repeating vortex rings. The plane of each ring was oriented at an angle (ψ) of $62.86 \pm 0.38^\circ$ ($N=132$) to the horizontal. This angle was used to estimate the relative contributions of vertical lift (L) and horizontal thrust (T) forces (Rayner 1979a,b), where:

$$L/T = \tan \psi. \quad (3)$$

Average L/T was calculated as 1.95 with a range of 1.33–3.73.

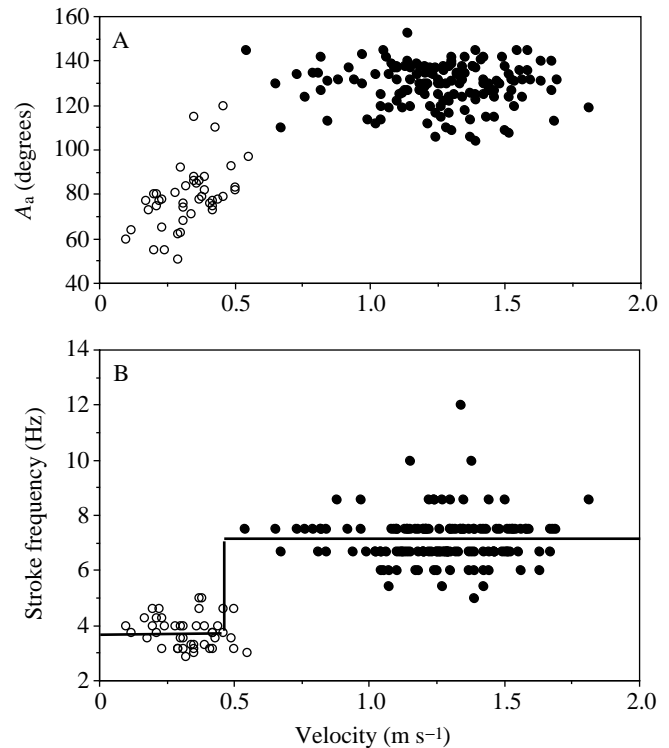


Fig. 3. Relationship of arc angle A_a (A) and frequency of stroke cycle (B) with velocity. Symbols represent paddling (open) and burst swimming (filled). (A) Paddling A_a increased linearly with velocity, U , according to the equation: $A_a = 55.62 + 70.54U$ ($r=0.53$). A_a was not influenced by U when ducklings were burst swimming. (B) Mean frequencies of the stroke cycle for paddling (3.78 Hz) and burst swimming (7.12 Hz) are shown by horizontal lines. The vertical line represents hull speed.

Discussion

Ducklings paddling at low speed act as displacement hulls and therefore encounter severe limitations owing to their small size. Although a few swimming sequences showed individuals swimming above U_{hp} , the distribution of swimming speeds showed that ducklings were speed-limited when paddling. The theoretical hull speed of 0.43 m s^{-1} for a 0.12 m duckling is 39% lower than the maximum sustained speed reported for 0.33 m adult ducks (Prange and Schmidt-Nielsen, 1970). Indeed, Clark and Fish (1994) found that maximum swimming speed in ducklings increased with body size.

High swimming speeds ($>U_{hp}$) by ducklings were not achieved by elevating the hull speed limit through an increase in l_w . U_{hb} was only 9% greater than U_{hp} ; whereas mean burst U was over 190% greater. If ducklings continued to act as displacement hulls, mean and maximum burst speeds could have been achieved only with l_w values of 1.02 m and 2.1 m, respectively.

To exceed U_{hp} by burst swimming, ducklings used a different mechanism for moving on the surface: they replaced the displacement hull configuration with a planing hull. A planing hull is designed to operate at high surface speeds. The

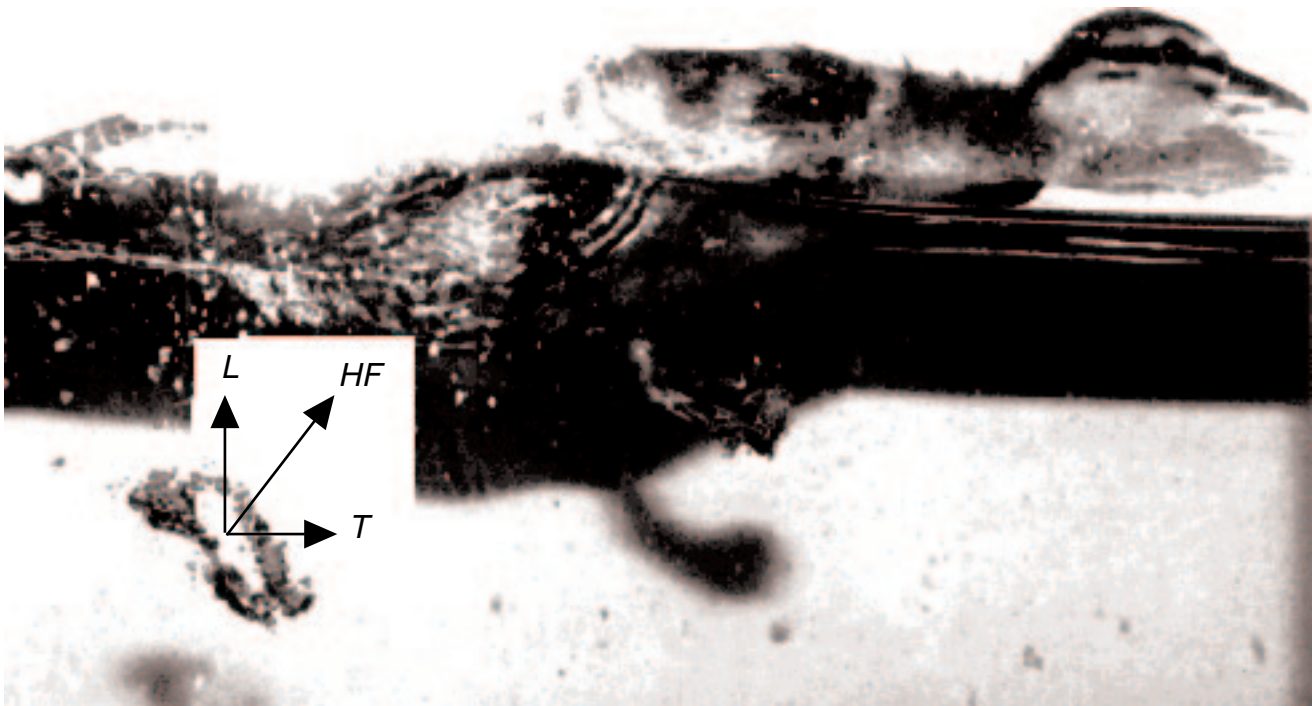


Fig. 4. Photograph of a hydroplaning duckling showing a ring vortex of air ventilated from the surface by the foot. The orientation of the plane of the vortex indicates the direction of the momentum jet. The momentum jet is used to show the direction of a hydrodynamic force (HF) that can be resolved into its lift (L) and thrust (T) components.

motion of a planing hull has been described as 'hydroplaning' or 'skimming' (Hammit, 1975). With the hull inclined with a positive angle of trim, a positive pressure develops under the hull, creating a force perpendicular to the long axis of the hull (Saunders, 1957; Marchaj, 1964). This normal force has a vertical component 'dynamic lift' which, at high speeds, may be greater than buoyancy. Furthermore, at high hydroplaning speeds, the hull effectively smoothes the water surface (Saunders, 1957).

Several factors contribute to the relatively low drag of planing. (1) The increase in trim angle raises the bow from the water, decreasing the amount of wetted surface area and reducing skin friction (Marchaj, 1964; Hammit, 1975). (2) Above hull speed, water does not have time to respond to the pressure disturbance and thus is not disturbed as much as at lower speeds (Taylor, 1933; Hammit, 1975). (3) Wave drag is largely eliminated by lifting the hull, although spray drag will increase (Saunders, 1957; Marchaj, 1964; Hoerner, 1965; Fish *et al.* 1991). In effect, the hull is 'outrunning' its own pressure disturbance (i.e. bow wave). This effect is analogous to an airplane moving at supersonic speed; the 'shock wave' is essentially the overlapping wave fronts created at the bow and stern (Giancoli, 1991).

Transition from displacement to planing in yachts depends on Froude number, hull design and displacement (Marchaj, 1964; Hammit, 1975). Planing starts at F values of approximately 0.6–0.89 (Saunders, 1957; Marchaj, 1964). At $F=0.6$ –1.0, a boat is supported by both hydrodynamic (dynamic lift) and hydrostatic (buoyant lift) forces (semi-

planing; Marchaj, 1964). Above $F=1.0$, the boat is supported entirely by dynamic lift (planing).

The duckling body has design features similar to hydroplaning hulls. To exploit dynamic lift, planing hulls have a flat underwater surface astern, a small length/beam ratio and a shallow draft (Saunders, 1957; Marchaj, 1964). The duckling's venter is relatively flat with a broad posterior region corresponding to the location of the hips. In general, ducks have a small length/width ratio. The canvasback (*Aythya valisineria*), redhead (*Aythya americana*) and lesser scaup (*Aythya affinis*) have length/width ratios of 3.77, 3.75 and 3.33, respectively (Lovvorn *et al.* 1991). Mallard ducklings have length/width ratios as low as 2. A low length/width ratio in concert with the high buoyancy from air in the plumage and respiratory system (Stephenson, 1993) provides the duckling with a shallow draft. However, the rounded sides of the duckling should reduce the planing surface effectiveness because of leakage of pressure from the underside (Marchaj, 1964).

The high velocities of burst swimming ducklings indicate that wave generation did not limit performance. Values for F and angle of trim showed that as ducklings exceeded hull speed they swam in the semi-planing and planing regimes (Fig. 5). The transition from displacement swimming to planing was accomplished by the forceful and extended sweeps of the webbed feet by either simultaneous or alternating movements. The result of this action was to propel the duckling over or through its own bow wave. Maintenance of increased vertical displacement of the duckling's body indicated that dynamic lift

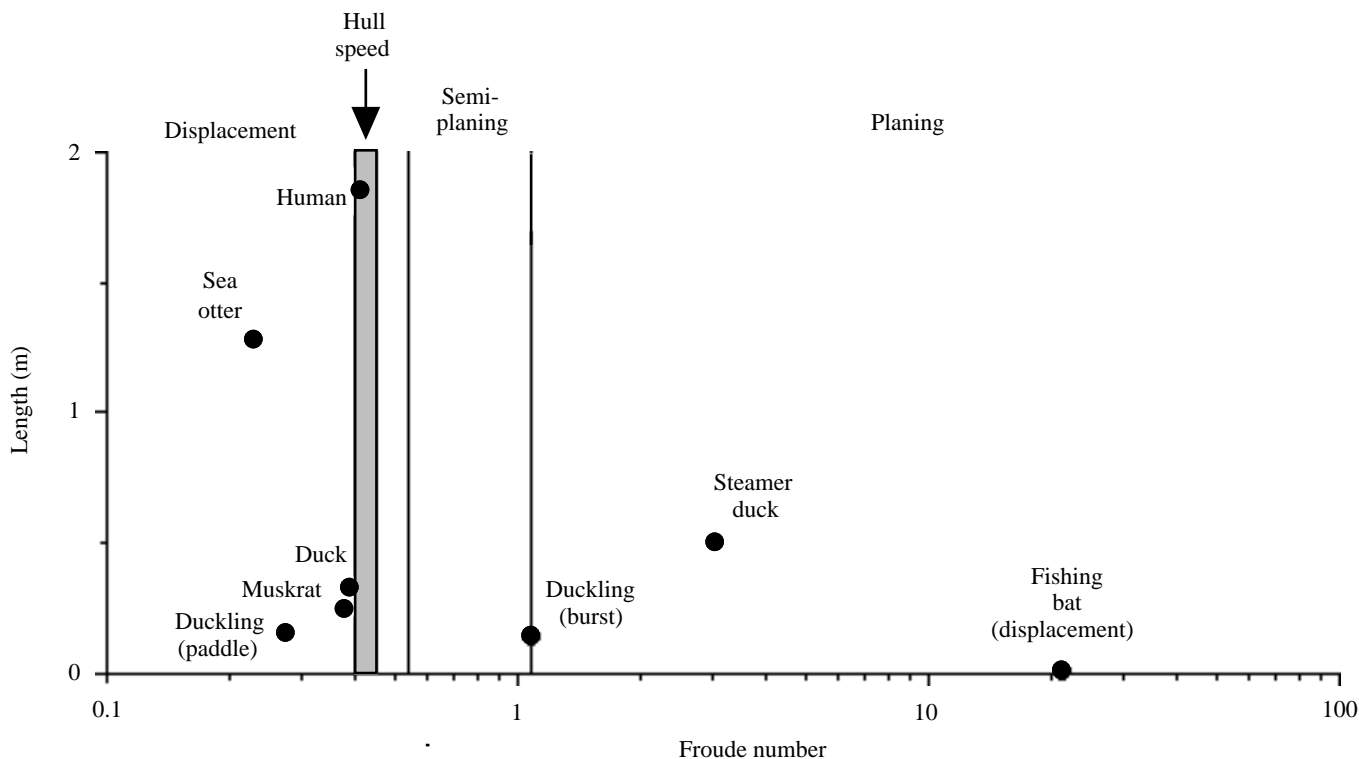


Fig. 5. Diversity of swimming performance for surface paddlers with respect to Froude number F . In cases where the waterline length l_w was unknown, body length was taken as l_w . Hull speed ranges from Froude numbers of 0.4 to 0.45. Maximum drag due to surface waves occurs at hull speed. Below hull speed, surface paddlers are analogous to displacement vessels, whereas as F increases above hull speed paddlers are able to hydroplane on the water surface. The toes of fishing bats are dragged at the water surface and therefore represent a displacement hull (Fish *et al.* 1991). While moving above hull speed, wave drag approaches zero (Hoerner, 1965). Data were obtained from Prange and Schmidt-Nielsen (1970), Fish (1982), Livezey and Humphrey (1983), Williams (1989), Fish *et al.* (1991), Kolmogorov and Duplishcheva (1992) and the present study.

was generated while planing. Although lift produced from the skimming body must have increased the height of the bird above the water surface, a major portion of the lift was generated from the paddling by the feet.

Vorticity visualized from ventilated air transported by the paddling feet indicated that a lift force was generated (Rayner, 1985). The vortices were concentrated into small, narrow-cored rings. Downward convection of the vortex rings generated lift as a reaction to the momentum transferred to the water. The lift was nearly twice the thrust force required to overcome the drag on the feet and skimming body. Similar vortex patterns for high lift have been observed in hovering and in slow flight (Rayner, 1985; Spedding *et al.* 1984; Rayner *et al.* 1986; Spedding, 1986). The magnitude of momentum carried by the vortex ring is proportional to the product of the ring's area and the vortex strength (Rayner, 1979a, 1985). To produce the same lift force as a large vortex ring, a small ring needs a greater induced velocity from the momentum jet (Rayner, 1979a). Accelerating a small mass of water to high velocity is less economical than the converse (Alexander, 1983). Such economic constraints possibly limit the use of lift generation for skimming by ducklings to short-term activities such as escape maneuvers. Larger size and increased propulsive area could foster extended use of skimming.

Steamer ducks (Anatidae; *Tachyeres* spp.) include three large, flightless species which propel themselves rapidly over the water surface using their feet and wings (Darwin, 1839; Murphy, 1936; Livezey and Humphrey, 1983). Steamer ducks swim continuously over distances of 1 km and at speeds up to 6.67 m s^{-1} (Murphy, 1936; Livezey and Humphrey, 1983). Assuming a waterline length 60% of total length, a steamer duck of 0.84 m (Murphy, 1936) would have an F value of 3.0 when swimming at maximum speed. This value would place the steamer duck in the planing regime (Fig. 5; Marchaj, 1964). Photographs of steamer ducks by Livezey and Humphrey (1983) show a positive angle of trim with the chest raised above the water surface. The simultaneous oarlike wingbeats in conjunction with the alternate paddling of the feet appear to increase the propulsive area for high-speed and sustained skimming.

The shift from displacement swimming to hydroplaning by ducklings requires a change in kinematics. The increased work performed by the feet might be accommodated either by increasing the arc through which the feet are swept or by increasing the stroke frequency. During sustained swimming, ducklings modulated the amplitude of the stroke but kept stroke frequency constant (Prange and Schmidt-Nielsen, 1970; Williams, 1983, 1989; Fish, 1984; Clark and Fish, 1994).

However, both A_a and frequency remained constant over the range of burst speeds. Therefore, the specific mechanism by which ducklings increase velocity once hydroplaning is achieved is unknown. The use of angular displacement data may be insufficient to determine stroke amplitude for animals with multi-jointed paddles. The distance traversed by the paddle may increase with speed while the angular displacement is maintained by control of the limb joints. High-performance undulatory swimmers use a dual-joint system in the peduncle to keep the angle of attack of the caudal propulsor constant over a majority of the stroke cycle (Fierstine and Walters, 1968; Fish *et al.* 1988; Fish, 1993).

The abrupt change in propulsive kinematics at hull speed by ducklings amounts to a change in gait (Alexander, 1989). Gait changes are associated with a reduction in the cost of transport, a reduction of peak force and increased efficiency (Heglund and Taylor, 1988; Alexander, 1989; Farley and Taylor, 1991; Carrier *et al.* 1994). Gait changes in vertebrates have primarily been examined for terrestrial locomotion, although gaits for flight and swimming have been considered more recently. The gaits of fish include median and paired fin propulsion, body and caudal fin propulsion, and escape responses (Webb, 1994). Porpoising by whales and dolphins is also considered to represent a swimming gait change (Alexander, 1989). However, prior to this study, gait changes have not been reported for surface-swimming paddlers.

For ducklings, the gait change observed is consistent with use of a two-gear muscle system. Muscles or motor units with contrasting performance optima would be recruited for either steady paddling or burst swimming (Goldspink, 1977; Rome *et al.* 1988; Webb, 1994). The transition between the two gaits appears to occur at the onset of hull speed. Farley and Taylor (1991) suggested that a musculoskeletal trigger switched at the gait transition and that this trigger operated at critical levels of force. For ducklings, that critical level of force would occur at the hull speed, where drag is maximal.

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