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RESEARCH ARTICLE

Aquatic burst locomotion by hydroplaning and paddling in common eiders (*Somateria mollissima*)

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ABSTRACT

Common eiders (*Somateria mollissima*) are heavy sea-ducks that spend a large portion of their time swimming at the water surface. Surface swimming generates a bow and hull wave that can constructively interfere and produce wave drag. The speed at which the wavelengths of these waves equal the waterline length of the swimming animal is the hull speed. To increase surface swimming speed beyond the hull speed, an animal must overtake the bow wave. This study found two distinct behaviors that eider ducks used to exceed the hull speed: (1) ‘steaming’, which involved rapid oaring with the wings to propel the duck along the surface of the water, and (2) ‘paddle-assisted flying’, during which the ducks lifted their bodies out of the water and used their feet to paddle against the surface while flapping their wings in the air. An average hull speed (0.732 ±0.046 $\mathrm{m\,s^{-1}}$) was calculated for *S. mollissima* by measuring maximum waterline length from museum specimens. On average, steaming ducks swam 5.5 times faster and paddle-assisted flying ducks moved 6.8 times faster than the hull speed. During steaming, ducks exceeded the hull speed by increasing their body angle and generating dynamic lift to overcome wave drag and hydroplane along the water surface. During paddle-assisted flying, ducks kept their bodies out of the water, thereby avoiding the limitations of wave drag altogether. Both behaviors provided alternatives to flight for these ducks by allowing them to exceed the hull speed while staying at or near the water surface.

KEY WORDS: Eider duck, Surface swimming, Ground effect, Hull speed, Steaming

INTRODUCTION

Animals swimming at the water surface face mechanical challenges that are distinct from those of submerged swimming. Similar to ships with displacement hulls, animals swimming at the surface must overcome waves generated by the displacement of water that results from their own forward locomotion (Prange and Schmidt-Nielsen, 1970; Fish, 1982; Williams, 1983, 1989; Fish et al., 1991; Aigeldinger and Fish, 1995; Fish and Baudinette, 1999). Differences in pressure around an animal’s body created by its movements produce bow and stern waves (Fig. 1) (Marchaj, 1964; Kay, 1971; Sorensen, 1973; Foley and Soedel, 1981). As an animal increases its swimming speed, the forward motion of the body causes the waves to constructively interfere, producing a wave with a wavelength equal to the waterline length of the animal (Marchaj, 1964; Aigeldinger and Fish, 1995). As a result, the body of the animal becomes trapped in a trough between the bow and stern waves (Fig. 1) (Fish, 1982; Fish and Baudinette, 1999). The speed at which the wavelength and the animal’s waterline length coincide, known as the hull speed, is an upper limit of speed for many animals that swim at the surface of the water (Kay, 1971; Vogel, 2003). The vertical displacement of water against gravity increases the drag on the body as kinetic energy from the animal is transferred to potential energy in the production of waves (Hertel, 1966; Prange and Schmidt-Nielsen, 1970; Sorensen, 1973). This increase in wave drag further limits the speed of the animal swimming at the air–water interface.

To exceed the hull speed, the animal must either plough through the bow wave or swim up over it; both methods are energetically expensive (Fish, 1982; Williams, 1983; Aigeldinger and Fish, 1995; Fish and Baudinette, 1999). However, once an animal exceeds the hull speed, it is in front of the waves that it produces. Mallard ducklings are able to exceed the hull speed by 2.7 times and hydroplane on the surface of the water by increasing the angle of their body with the water surface, generating lift with their feet by increasing paddling frequency (Aigeldinger and Fish, 1995). Steamer ducks are thought to be able to hydroplane on the surface of the water, and reported speeds indicate that they likely exceed their hull speed, although this has not been tested directly (Humphrey and Livezey, 1982; Livezey and Humphrey, 1983, 1986).

The common eider, *Somateria mollissima* (Linnaeus 1758) is a large, heavy marine duck (Johnsgard, 1965) found along the coastlines of North America and northern Europe (Watson et al., 1993; Desholm et al., 2002; Ouellet et al., 2008). The high body weight of the ducks limits their ability to fly, as their wing loading (the ratio of body mass to wing area) is close to values seen in flightless or near-flightless birds (Goudie and Ankney, 1986; Guillemette et al., 2007). Prior to laying their eggs each year, mature female eiders gain even more weight, causing them to exceed the wing loading threshold for flight and become temporarily flightless (Guillemette and Ouellet, 2005a,b). Their heavy bodies allow the ducks to dive deeply to forage on benthic invertebrates, predominately sessile blue mussels (Guillemette et al., 1992). However, their reduced capacity for flight could leave eider ducks vulnerable to predators on the surface of the water.

To move rapidly at the water surface, common eiders can perform one of two distinct behaviors: steaming and paddle-assisted flying, which have both been referred to as ‘skittering’ (Storer, 1952; Stewart, 1958; Thoresen, 1964; Raikow, 1973; Humphrey and Livezey, 1982). However, use of the wings for the two behaviors differs substantially, indicating that these are two distinct methods of locomotion. Steaming involves oaring through the water with the wings, typified by the behavior of steamer ducks (Humphrey and Livezey, 1982; Livezey and Humphrey, 1983, 1986). Paddle-assisted flying involves paddling along the surface of the water with the feet while the wings are flapped without contacting the water. The goals of this study were to quantify

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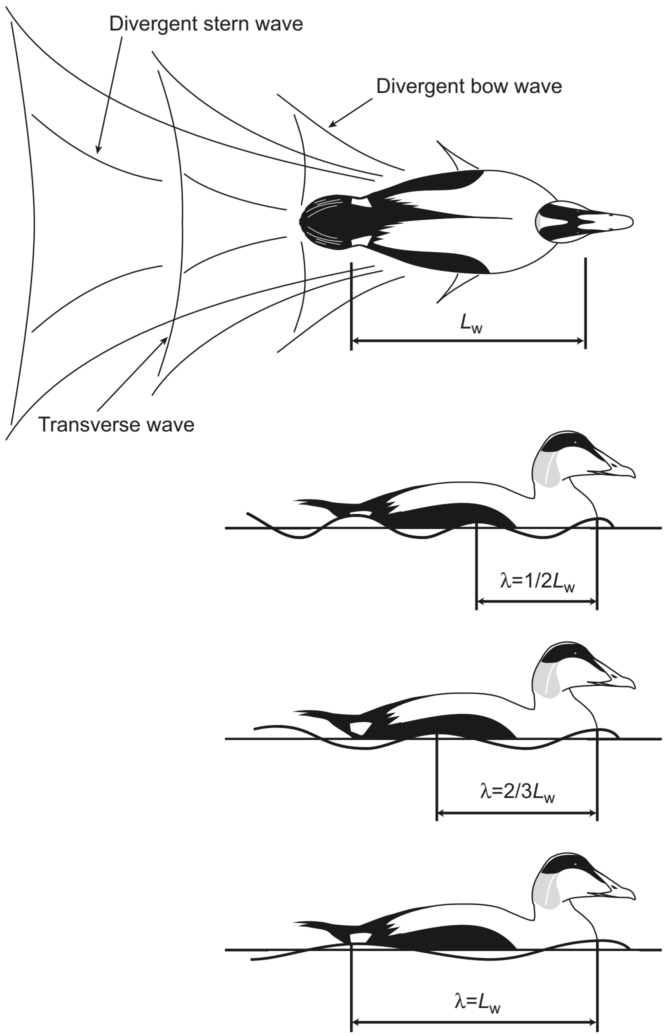

Fig. 1. Diagram of the divergent and transverse waves produced by a duck as it moves at the water surface from dorsal (top) and lateral (bottom) views. The maximum waterline length (L_w) represents the length of the duck in contact with the water, from the base of the neck to the base of the tail. The wavelength (λ) of the surface wave increases as the duck builds speed. The point where the wavelength equals the waterline length is the hull speed. At the hull speed, the duck is effectively trapped in a wave trough, limiting surface swimming speed. In the lateral views, the lines in the wake represent the bow wave (solid curved line) relative to the undisturbed water line (solid horizontal line). Modified from Marchaj (1964).

the kinematics and performance of common eiders for these two behaviors and to determine whether they allow eiders to exceed their predicted hull speed.

RESULTS

Average daily wind speed during video data collection ranged from 1.15 to 4.1 m s^{-1} and originated from the northwest at an average angle of 300.5 deg. Sea state was coded between 0 (glassy) and 2 (wavelets). Ducks did not appear to orient with respect to wind or wave direction.

High-speed video data were collected for 128 sequences of eider ducks steaming (N=37), paddle-assisted flying (N=73) or flying (N=18). Fig. 2 contains a series of still images recorded during a single steaming wingbeat cycle (Fig. 2B–E). At the end of the upstroke, the wings were held with the antebrachia oriented vertically and the manus pointed slightly caudally (Fig. 2B). The average angle between the antebrachia of each wing at the end of the upstroke was measured from a posterior view to be 301.1±18.4 deg (Fig 3; N=3). From this position, the ducks began the downstroke by extending the manus and the antebrachia. The wings were rotated forward and the leading edge was pitched downward (Fig. 2C) as the wings were adducted cranially and ventrally towards the water surface until the antebrachia and manus were submerged. Once the antebrachia and manus were below the surface, the ducks adducted the wings caudally in an oaring motion (Fig. 2D). The average angle between the brachia at the end of the downstroke was 100.3±25.4 deg (Fig. 3; N=3). At the end of the downstroke, the ducks pitched the leading edge of the wings up slightly and then abducted the wings dorsally and cranially until the antebrachia and manus were completely clear of the water (Fig. 2E). Splashing by the wings obscured any motions by the feet during steaming, so it was not possible to directly observe foot movements.

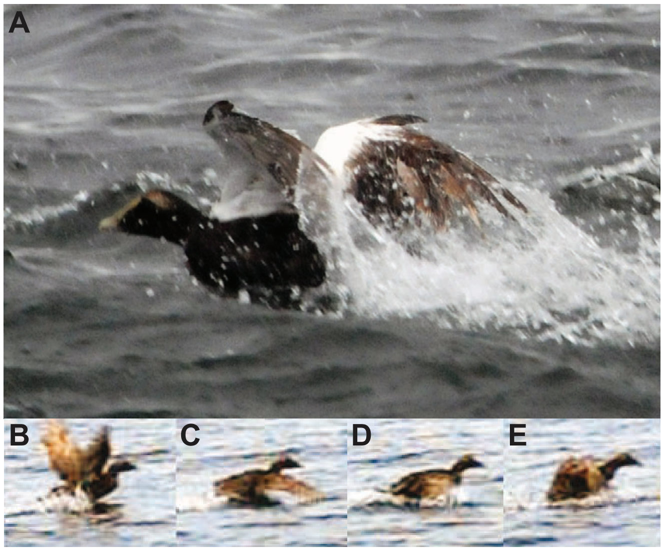

Fig. 2. Images of ducks seen from a lateral perspective performing the steaming behavior at the water surface. (A) High resolution image. (B–E) Image sequences over one wingbeat cycle. (B) The wings are held vertically and extended at the end of the upstroke. (C) The wings rotate forward and are pitched downward toward the water surface. (D) The antebrachia and manus are submerged and begin to abduct caudally. (E) The wings are pitched upwards and brought out of the water.

During steaming, the ducks oared their wings through the water to build speed, while keeping their body in contact with the water surface. The head was canted forward and the neck extended. The average body angle relative to the water surface during steaming was 16.4±7.5 deg (N=9). This posture differs from when the ducks are routinely paddling with a vertical orientation of the head and neck. The average maximum waterline length for steaming was measured as 34.5±4.2 cm (N=23) from museum specimens. From this, the hull speed was calculated as 0.732±0.046 m s^{-1}. The average speed of a duck during steaming was 3.99±1.02 m s^{-1} (N=38), which is 5.5 times faster than the calculated hull speed. The Froude number of a duck traveling at this speed was calculated to be 2.17.

During paddle-assisted flying, the ducks flapped their wings while their feet alternately paddled at the water surface. The posture was similar to that of flight, with the head and body extended and held parallel to the water surface. Fig. 4 contains a series of still images recorded during a single wingbeat cycle of paddle-assisted flying (Fig. 4B–E). At the end of the upstroke, the wings were held

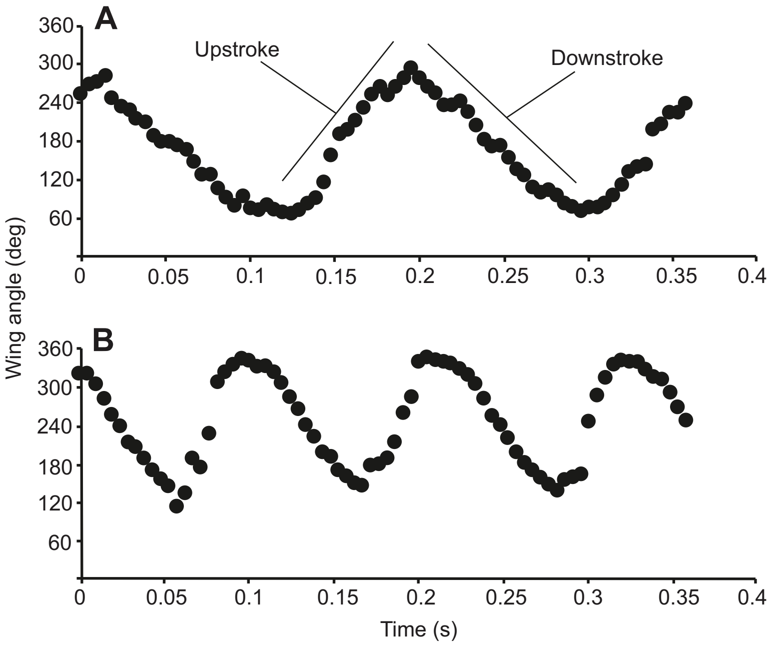

Fig. 3 Angle of the wings over the course of multiple wingbeat cycles for steaming and paddle-assisted flying. (A) Steaming; (B) paddle-assisted flying (running). Each point represents the angle of the wings at a single frame measured from a posterior view of the duck. A measured angle of 0 deg would occur if the duck's wingtips touched ventrally, while 360 deg would occur if the wingtips touched together dorsally.

vertically and both the antebrachia and manus were extended (Fig. 4B). The average wing angle between the antebrachia at the end of the upstroke was measured from a posterior perspective to be 332.8±8.6 deg (Fig. 3; *N*=5). The ducks began each downstroke by adducting the wings ventrally towards the water surface and slightly cranially (Fig. 4C). When the brachia reached a horizontal position, they were rotated forward to tip the antebrachia of each wing downward at the end of the downstroke. The average angle between the antebrachia at the end of the downstroke from a posterior view was measured to be 148.4±10.9 deg (Fig. 3; *N*=5). The motion of the brachia caused the antebrachia and manus to continue moving ventrally and medially. The wing tips came in close proximity to, but never touched, the water surface at the end of the downstroke (Fig. 4D). The ducks began the upstroke by moving the wings upward at the brachia (Fig. 4E). As the brachia were moved vertically, the antebrachia and manus were moved upward, extending the wings at the end of the upstroke. Simultaneously, the duck's feet were performing a continuous, alternating paddling motion. As one foot was fully extended beneath the surface of the water, the other foot was positioned close in to the body. The extended foot contacted the surface of the water with webbing fully spread (Fig. 4C). The average speed of a duck during paddle-assisted flying was 4.95±1.31 m s^{-1} (*N*=5).

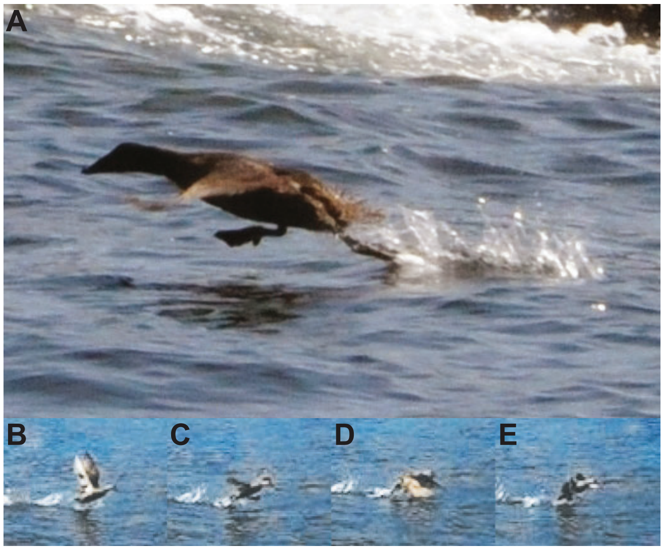

Fig.4. Images of ducks seen from a lateral perspective performing the paddle-assisted flying behavior at the water surface. (A) High resolution image. (B–E) Image sequences over a single wingbeat cycle. (B) The wings are held vertically and extended with the tips almost touching at the end of the upstroke. (C) The wings are adducted ventrally and caudally towards the water surface until they are horizontal. The duck's foot is visible as it extends towards the water. (D) The wing tips come in close proximity to the water surface at the bottom of the downstroke. (E) The brachia are pulled upward at the beginning of the upstroke.

The mean duration of each wingbeat cycle was measured for steaming (0.222±0.022 s, *N*=37), paddle-assisted flying (0.115±0.007 s, *N*=73) and flying (0.123±0.007 s, *N*=18) ducks. The frequency of the wingbeat cycle was 4.5, 8.7 and 8.1 Hz for steaming, paddle-assisted flying and flight, respectively. The variances and sample sizes of the three locomotor modes were not equal, so a Welch's ANOVA was used in conjunction with a Games–Howell *post hoc* test. The Welch's ANOVA showed significant differences among the wingbeat cycle durations of the three behaviors (*F*=758.373, *P*<0.0001; Fig. 5). The Games–Howell test showed significant differences between steaming and paddle-assisted flying (0.107±0.004, *P*<0.0001), steaming and flying (0.099±0.004, *P*<0.0001), and paddle-assisted flying and flying (0.007±0.002, *P*=0.004).

The angle between the antebrachia was significantly higher during paddle-assisted flying than during steaming at the end of the upstroke (*t*=−2.797, *P*=0.0413) and at the end of the downstroke (*t*=−3.112, *P*=0.0345). The average angular velocity was 2510.5 deg s^{-1} for steaming and 4321.9 deg s^{-1} for paddle-assisted flying. A *t*-test showed a significant difference between the average angular velocities of the two behaviors (*t*=4.3811, *P*=0.0047).

DISCUSSION

Flight is typically an ideal rapid escape behavior for an aquatic bird. However, a number of seabirds, such as cormorants, auks and sea ducks, have high wing loadings that make taking off from water difficult (O'Farrell et al., 2002). The common eider has an

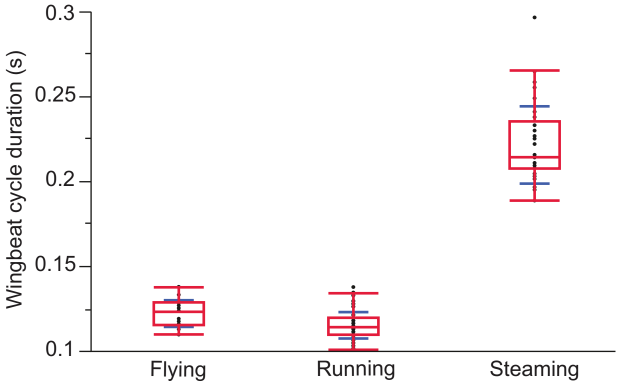

Fig. 5. ANOVA showing the duration of a wingbeat cycle for flying, paddle-assisted flying (running) and steaming. The red box-and-whiskers plot represents the mean, quartiles, minimum and maximum for each behavior. The blue lines above and below the quartiles represent the s.d. for each behavior. Each point represents the mean duration over three consecutive cycles for a duck performing one of the three behaviors. All three behaviors are significantly different (steaming and paddle-assisted flying, $P<0.0001$; steaming and flying, $P<0.0001$; paddle-assisted flying and flying, $P=0.004$).

exceptionally high wing loading relative to other marine birds. Flightlessness is most often observed in birds with wing loadings above 2.25 g cm^{-2} (Meunier, 1951; Humphrey and Livezey, 1982; Guillemette and Ouellet, 2005a). The wing loading for the common eider is reported to range from 1.5 to 2.8 g cm^{-2}, which is close to or exceeds the threshold for flightlessness (Ouellet et al., 2008; Guillemette and Ouellet, 2005a). Wing loading in eider ducks can be particularly high when a large mass of food is ingested, while females are carrying eggs, during molting and prior to fledging (Guillemette, 1994; Guillemette and Ouellet, 2005a,b; Guillemette et al., 2007; Watanabe et al., 2011). As a result, common eiders must often rely on behaviors other than flight for rapid escape, such as diving under the water or moving rapidly along the surface. Steaming and paddle-assisted flying are common behaviors that provide a quick escape and may cause confusion in surface predators (Thoresen, 1964). Surface swimming may also aid in avoiding aquatic predators, such as seals, to which they are more vulnerable during dives (Guillemette and Ouellet, 2005b).

The duration of a single wingbeat cycle was longer in steaming than in paddle-assisted flying and flight (Fig. 3). This relatively slow wingbeat speed in steaming is likely due to the increased resistance of moving a broad wing through the denser medium of water as opposed to air. At the end of the upstroke, the angle between the left and right wings relative to one another remained larger during steaming than during paddle-assisted flying (Fig. 3). Keeping the wings slightly bent and closer to the water surface may reduce the time for the duck to initiate another wing stroke. Bringing the wings up and orienting them vertically would add time to the wingbeat cycle and would be unnecessary, as the wings are not primarily being used to produce aerial lift.

There was no reliable method of determining which behavior a duck would display when approached, but we generally observed more paddle-assisted flying events than steaming events. The high speeds obtained and the reduced wave drag incurred during paddle-assisted flying would presumably make it preferable to steaming. However, it is possible that maintaining a position above the water surface incurs a high cost of transport for paddle-assisted flying ducks due to their high wing loadings. For higher wing loadings, short distance flights can incur high energy costs and decreased velocity during takeoffs (Nudds and Bryant, 2000, 2002). Therefore, steaming may present a low-cost and rapid alternative to flight that allows for increased speeds that are still above hull speed.

Steaming in common eiders and other species

By steaming at the surface of the water, common eiders are able to move 5.5 times faster than their predicted hull speed. Strokes by the wings and likely the feet allow eider ducks to generate sufficient thrust and lift to exceed the predicted hull speed. The duck is able to avoid being trapped in a trough between the crests of the bow and stern waves by swimming up and over the bow wave, remaining ahead of the bow wave until speed is reduced again. 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 (Aigeldinger and Fish, 1995). Wave drag increases steeply with increasing speed up to the hull speed and becomes the dominant drag component as the hull speed is approached (Hertel, 1966; Sorensen, 1973). However, by climbing over the bow wave, the duck is able to mitigate the wave drag.

The average Froude number for steaming eider ducks was 2.17. A Froude number of 0.4–0.45 coincides with the maximum wave drag at hull speed for a displacement hull, like a ship or duck body (Hoerner, 1965; Aigeldinger and Fish, 1995; Vogel, 1988, 1996; Fish and Baudinette, 1999). Hydroplaning starts at a Froude number of approximately 0.6–0.89 (Fig. 6) (Saunders, 1957; Marchaj, 1964). Between Froude numbers of 0.6 to 1.0, a planing vessel is supported by both hydrodynamic (dynamic lift) and hydrostatic (buoyant lift) forces (semi-planing; Marchaj, 1964). Above a Froude number of 1.0, the vessel skims on the surface of the water, where the speed and shape of the hull generate enough dynamic lift to support the weight of the vessel (i.e. planing or skimming; Marchaj, 1964). The dynamic lift is generated as the hull is 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). The vertical component of the normal force is the dynamic lift. At planing speed, the center of gravity rises above its position when the hull is at rest (Saunders, 1957).

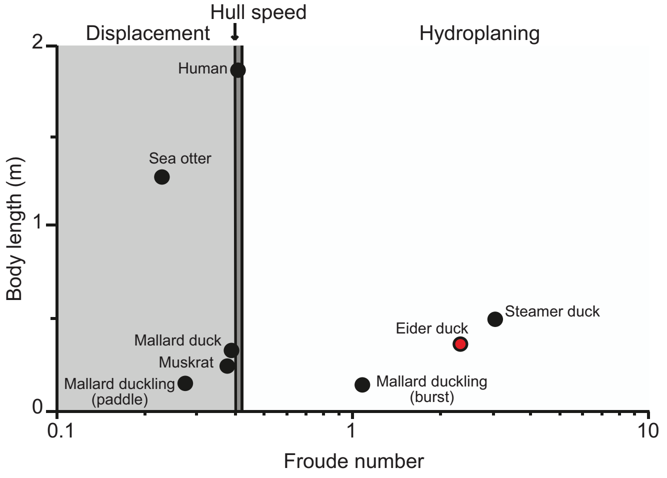

Fig. 6. Comparison of swimming performance for species swimming at the water surface. Common eiders are shown as a red point. Hull speed occurs at a Froude number of 0.4–0.45; below this range, the swimmer acts like a displacement hull, while a Froude number of 0.6–1.0 is considered to be semi-planing as the body is supported by both hydrodynamic and hydrostatic lift forces. Above a Froude number of 1.0, the body is supported solely by hydrodynamic lift and hydroplanes along the surface. Modified from Aigeldinger and Fish (1995).

The high speed and positive body angle (between 5 and 25 deg) of the eider ducks in this study could contribute to the production of dynamic lift, along with lift from the wings and the feet, which would support the weight of the duck and raise the animal higher out of the water than would be expected from a buoyant force alone (Aigeldinger and Fish, 1995). A high body angle also decreases the waterline length, reducing the frictional drag on the body through a reduction in wetted surface area (Marchaj, 1964). At high hydroplaning speeds, the hull effectively smoothes the water surface (Saunders, 1957), further mitigating wave drag.

The ability to hydroplane has been described for other species of ducks. Hochbaum (1944) reported that flightless adult canvasback ducks (*Aythya valisineria*) could move at the surface of the water at speeds between 3.5 and 4.5 m s^{-1}. Wood duck (*Aix sponsa*) ducklings could swim at 2.6 m s^{-1} (Stewart, 1958), which was 50% faster than observed for hydroplaning mallard ducklings (*Anas platyrhynchos*; Aigeldinger and Fish, 1995). Members of the Alcidae, including murres (*Uri*), guillemonts (*Cepphus*), puffins (*Fraterculus*) and auklets (*Cerorhinca* and *Ptychoramphus*), were found to use a similar steaming behavior as a lead-in to other taxiing behaviors (Storer, 1952; Mackenzie, 1987; Boag and Alexander, 1995). In the process of collecting data for this study, a black guillemot (*Cepphus grille*) was observed to use its wings to surface swim at 7.6 m s^{-1}.

Steaming behaviors, similar to those found for eider ducks, have been described in steamer ducks (Anatidae; *Tachyeres* spp.; Livezey and Humphrey, 1983) and mallard ducklings. Steamer ducks include three large, flightless species (Darwin, 1839; Murphy, 1936; Livezey and Humphrey, 1983). Steamer ducks received their name for their wing movements that mimic a steamer barge's circular oar. Because of similarities with this behavior, we describe the oaring behaviors seen in the common eider as 'steaming'. This wing paddling action of the steamer duck is supplemented by strong foot paddling (Livezey and Humphrey, 1983; Reynolds, 1934). Using this behavior, steamer ducks can swim continuously over distances of 1 km and at speeds up to 6.67 m s^{-1} (Murphy, 1936; Livezey and Humphrey, 1983). The bones and muscles of the wings of steamer ducks are considered to be stouter and more robust than those of flying birds (Lowe, 1934). Mallard ducklings also exhibit a wing-paddling behavior that is similar to steaming (Aigeldinger and Fish, 1995; Dial and Carrier, 2012). Like steamer ducks and eider ducks, mallard ducklings have high wing loadings, but in their case this is due to slow development of the wings relative to the precocial development of the hindlimbs (Dial and Carrier, 2012). This wing-paddling behavior is most pronounced between day 30 and day 60 of their development, after which the wings are more fully developed and suited for flight (Dial and Carrier, 2012; Dial et al., 2012). However, we observed wing-paddling in mature adult eiders. We also recorded steaming behaviors in some sub-adult common eiders, and although we were not able to measure kinematics from these videos to compare with adults, the observation of this behavior during ontogeny indicates that it may be a pre-flight behavior that is retained after fledging.

Paddle-assisted flying in common eiders and other species

Common eiders were not limited to steaming to rapidly locomote at the water surface. The ducks often engaged in paddle-assisted flying, which allowed them to move 1.2 times faster than steaming and 6.8 times faster than the predicted hull speed. During this behavior, the feet paddled against the surface of the water in an alternating pattern as the wings flapped to help maintain speed and generate lift. This combination of aerial locomotion and aquatic paddling allowed the duck to avoid bodily contact with the water, thus eliminating wave drag and allowing faster locomotion.

Behaviors similar to paddle-assisted flying have been described for a number of species of aquatic birds. Most of these species use this surface behavior to 'taxi' before takeoff (Mackenzie, 1987; Norberg and Norberg, 1971). In the process of collecting data for this study, cormorants and gulls were observed using simultaneous movements of the feet to accelerate while taking off from the water. Puffins have been described as 'skittering' across the water, which implies the use of alternating foot movements for a similar purpose (Roots, 2006). Loons, coots, shearwaters, albatrosses, guillemots and various duck species have been observed using alternating foot movements and wing flapping to achieve lift while taking off (Mackenzie, 1987; Norberg and Norberg, 1971). The red-throated diver (*Gavia stellata*) uses paddle-assisted flying to achieve speeds of up to 10 m s^{-1} as it takes off from the water (Norberg and Norberg, 1971). However, we only occasionally observed paddle-assisted flying to result in takeoff into flight, and therefore it is likely not exclusively a taxiing behavior in the common eider.

The wing movements during paddle-assisted flying are very similar to the movement of the wings during flight (Brown, 1951). In the case of flight, most of the lift is generated during the downstroke (Brown, 1951; Dial et al., 1988; Poore et al., 1997) and, because of similarity in kinematics, we would expect the same to be true in the case of paddle-assisted flying. Paddling the feet in the water could help to keep the ducks aloft by producing a downward oriented component of force (Aigeldinger and Fish, 1995; Bush and Hu, 2006) throughout the wingbeat cycle. In addition, the wings could generate increased lift through ground effect interactions at the air–water interface (Hurt, 1965; Blake, 1983; Rayner, 1991; Zerihan and Zhang, 2000; Finn et al., 2012; Su et al., 2013). Ground effect occurs between a wing and an incompressible surface when the air flow underneath the wing interrupts the formation of the wing tip vortex (Blake, 1983). This action reduces the drag on the wing induced by this vortex and generates greater lift. Therefore, the ground effect can reduce the energy cost of locomotion for birds with high wing loading. Large birds and birds with high wing loadings are considered to use ground effect during takeoffs over water with extended taxiing (Withers and Timko, 1977; O'Farrell et al., 2002), and eider ducks may be taking advantage of this phenomenon during non-taxiing paddle-assisted flying.

Ground effect depends on the ratio (β) of the height of the wings above the water surface (h) to half the wing span (b) (Rayner, 1991). Above $\beta=1$, ground effect has little effect, but when $\beta=0.5$ the savings in power for flight are greater than 10%. Further power savings of up to 30% occur at $\beta=0.2$–0.3. The observation of eider ducks flying close to the surface of the water (O'Farrell et al., 2002) indicates that these birds could use ground effect. Eider ducks were observed to fly with the body less than 25 cm above the water surface with the wing tips no more than 1–2 cm above the surface at the end of the downstroke (O'Farrell et al., 2002). For an eider duck with a wing length of 28.9 cm (Greenewalt, 1962), h for $\beta=0.5$ would be 14.5 cm. Wing heights of this value and lower were observed in the present study, indicating probable use of ground effect during paddle-assisted flying. Furthermore, the flapping of the wings can enhance thrust and lift production due to ground effect (Molina and Zhang, 2011; Quinn et al., 2014).

Conclusions

Steaming and paddle-assisted flying are distinct behaviors that allow common eiders to overcome the limitations of hull speed that are faced by species that swim at the water surface. Terms such as ‘skittering’ have been used to describe a variety of rapid surface behaviors performed by aquatic birds, but we have identified distinctions that allow us to consider advantages of specific behaviors. The combined use of paddling feet and wings during steaming permits the ducks to hydroplane on the surface of the water. In paddle-assisted flying, the ducks are able to combine wing flapping and paddling with ground effect to keep the body above the water surface and rapidly locomote. Both behaviors are mechanisms for burst locomotion at the surface of the water that serve as alternatives to diving or flight for these heavy marine ducks.

MATERIALS AND METHODS

This study on common eiders (*S. mollissima*) was carried out in the waters of the Gulf of Maine near the Isles of Shoals (42°59.205′, 70°30.877′) from late July to early August for three successive years (2012–2014). All data were collected between 11:00 h and 17:00 h. Wind speed and direction were determined from data obtained from the National Data Buoy Center of the National Oceanic and Atmospheric Administration (http://www.ndbc.noaa.gov). Sea state was determined based on the World Meteorological Organization sea state code (http://www.wmo.int/pages/prog/amp/mmop/faq.html). Specific days and times were chosen for data collection based on a visible lack of wind and wave activity.

Single individuals and groups of ducks ranging in size from two to >100 individuals were recorded with high-speed video as they performed escape maneuvers. Video recordings of ducks were made from a motorized inflatable boat using a Casio Exilim FH20 recording at 210 frames s^{-1} with a resolution of 480×360 pixels. The shutter speed was set automatically by the camera and could be as high as 1/2000 s. When the boat was pacing a focal duck, the speed was measured with a hand-held GPS unit (Garmin GPSmap 78). Instability of the boat during filming and distance of the ducks from the camera made absolute identification of each duck difficult, especially within large groups of over 100 ducks. As much as possible, kinematics of individual ducks were only measured once per analysis, although, in rare cases, the same individual may have been measured more than once.

Video recordings were analyzed frame-by-frame using ImageJ (Rasband, 2012). Data obtained from videos included wingbeat frequency (Hz) and duration of the wingbeat cycle (s). The average duration of a wingbeat cycle for an individual duck was determined as the average of three consecutive wingbeats. Posterior views of the ducks were used to measure the angle between the wings at the end of the upstroke and the end of the downstroke (Fig. 4) as well as angular velocity (deg s^{-1}). Lateral views of the ducks were used to measure the angle of the body relative to the water surface.

The average maximum waterline length for eider ducks was measured from 23 adult specimens at the Delaware Museum of Natural History and the Cornell University Museum of Vertebrates as the ventral length from the base of the neck to the base of the tail. This measurement was used to calculate a predicted hull speed (U_h) using the following equation:

$$U_\mathrm{h} = \left(\frac{\boldsymbol{g}L_\mathrm{w}}{2\pi}\right)^{\frac{1}{2}}, \qquad (1)$$

where $\boldsymbol{g}$ is the acceleration due to gravity (9.8 m s^{-2}) and L_w is the maximum waterline length of the duck. This equation is usually used to predict the celerity of gravity waves (Denny, 1988). The Froude number was calculated according to the equation:

$$F = \frac{U}{\sqrt{\boldsymbol{g}L_\mathrm{w}}}. \qquad (2)$$

Froude number represents the ratio of inertial to gravitational forces of a body moving at the surface of the water (Webb, 1975). Hull speed occurs at a Froude number around 0.40–0.45 (Hoerner, 1965; Vogel, 1988; Aigeldinger and Fish, 1995). If the Froude number is higher than 1.0, the animal is considered to be hydroplaning (Marchaj, 1964; Aigeldinger and Fish, 1995).

Data were analyzed statistically using JMP (ver. 10.0.0) and SPSS (ver. 17.0). Variation about means was expressed as ±1 s.d. Wingbeat duration for steaming, paddle-assisted flying and flying was compared using Welch’s ANOVA and the Games–Howell *post hoc* test. Wing angle was compared using one-tailed *t*-test performed in JMP. Statistical significance was set at a level of $P<0.05$.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
F.E.F. conceptualized and supervised the project. W.T.G., S.C.F. and F.E.F. collected data in the field. W.T.G. performed video analysis. W.T.G. and S.C.F. ran statistical tests. W.T.G., S.C.F. and F.E.F. prepared the manuscript and figures.

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