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Foot-propelled swimming kinematics and turning strategies in common loons

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Loons are expert swimmers, capable of diving over 70 m to capture fish. Here we reveal the secrets of how loons swim and maneuver using only their feet.

Abstract (249 words, 250 max)
Loons (Gaviiformes) are arguably one of the most successful groups of swimming birds. As specialist foot-propelled swimmers, loons are capable of diving up to 70 meters, remaining underwater for several minutes, and capturing fish. Despite the swimming prowess of loons, their undomesticated nature has prevented prior quantitative analysis. Our study used high-speed underwater cameras to film healthy common loons (Gavia immer) at the Tufts Wildlife Clinic in order to analyze their swimming and turning strategies. Loons swim by synchronously paddling their feet laterally at an average of 1.8 Hz. Combining flexion-extension of the ankle with rotation at the knee, loon swimming resembles grebe swimming and likely generates lift forces for propulsion. Loons modulate swimming speed by altering power stroke duration and use head-bobbing to enhance underwater vision. We observed that loons execute tight but slow turns compared to other aquatic swimmers, potentially associated with hunting by flushing fish from refuges at short range. To execute turns, loons use several strategies. Loons increase the force produced on the outside of the turn by increasing the speed of the outboard foot, which also begins its power stroke before the inboard foot. During turns, loons bank their body away from the turn and alter the motion of the feet to maintain the turn. Our findings demonstrate that foot-propelled swimming has evolved convergently in loon and grebes, but divergently from cormorants. The swimming and turning strategies used by loons that allow them to capture fish could inspire robotic designs or novel paddling techniques.
Introduction

Loons excel at swimming, paddling their feet to dive underwater for more than 70 meters (Schorger, 1947). They survive by capturing fish, a skill that requires a high level of maneuverability and speed. Yet, loons evolved from birds that use the hindlimbs for walking on land, repurposing their legs as paddles. Although producing propulsive forces underwater poses distinct physical challenges from walking, several independent lineages of birds have evolved foot-propelled diving, including grebes, cormorants, seaducks, and extinct Hesperornithiformes (Zinoviev, 2011). Within extant foot-propelled diving birds, loons demonstrate a strong preference for large bodies of water and a particular intolerance for captivity. As a result, loon swimming has never been quantitatively studied. Yet, as one of nature’s most agile foot-based swimmers, loons offer valuable insight into successful strategies for swimming and maneuvering underwater by means of foot-propelled paddling.

Diving birds face specific physical challenges to power underwater locomotion, leading to varying levels of specialization within foot-propelled diving birds. The most recent common ancestor of all extant birds was able to walk and fly, passing on to its descendants anatomical features to support the body against gravity while on land and reduce body mass for flight (such as hollow bones, Johnsgard, 1987). Yet, many of these characters limit swimming performance. All swimming birds must overcome buoyancy to dive, with adaptations to increase body density such as wettable feathers (Grémillet et al., 2005) or solid bones (Chinsamy et al., 1998). Birds that swim using their feet encounter particular physical challenges associated with the hindlimbs. The propulsive force generated by a foot depends on its speed, shape, and surface area (Vogel, 2008). To maximize force, many foot-propelled birds have webbed or lobed toes, but large feet may make walking on land cumbersome. Due to these conflicting functional pressures on the hindlimb, foot-based diving birds face a trade-off with walking. As a result, foot-propelled swimming has independently evolved to differing levels of specialization, from many cormorants and seaducks that regularly spend time on land (Abourachid, 2001; White et al., 2008) to grebes and loons that can barely stand on solid ground (Johnsgard, 1987).

The loon family includes five extant, Holarctic species, including the common loon (Gavia immer), which breeds on lakes in northern North America and winters along the North American coasts (Johnsgard, 1987). Loons spend almost their entire life on the water, only venturing on land to build and tend a nest near the shoreline. The common loon has been caught
in fishing nets dozens of meters below the surface (Schorger, 1947) with diving durations recorded of over two minutes (Nocera and Burgess, 2002). However, loons prefer large territories (Barr, 1996), and adults do not survive well in captivity (Miller and Fowler, 2014). The technical challenges of studying loon swimming have impeded any prior analysis of how loons produce the forces necessary to swim using their feet.

Foot-based swimming has historically been considered to rely on drag force production (Blake, 1981), though recent studies of other specialized diving birds suggest an ability to generate lift forces. Steady fluid forces can be categorized into drag and lift. Drag forces resist motion through a fluid, acting opposite to the direction of movement and parallel to incident water flow. In contrast, lift forces act perpendicular to the incident water flow over a propulsive appendage. Previously, swimming using the feet was considered drag-based, with the foot paddling backwards to power forward motion (Baudinette and Gill, 1985; Blake, 1981; Fish, 1996; Vogel, 2008). Yet recent studies of cormorant and grebe swimming show that the feet of specialized diving birds do not move backwards relative to still water, and therefore likely power swimming more through lift- than drag-based forces (Johansson and Norberg, 2000, 2001 and 2003; Ribak et al., 2004). However, grebes and cormorants likely use different mechanisms for producing lift due to divergence in the shape of the feet and orientation of the limb while paddling. With feet that resemble those of cormorants but exhibiting a similar level of aquatic specialization to grebes, how does loon swimming compare to that of cormorants and grebes? Do loons also exhibit signs of producing lift forces for underwater propulsion?

To successfully capture prey, specialized foot-propelled diving birds must not only power straight swimming but also be highly maneuverable. All previous studies of foot-propelled diving birds restricted subjects to a straight tunnel, though one study included a single vertical obstacle (Johansson and Norberg, 2001; Ribak et al., 2004; Ribak et al., 2008). While informative, such experiments do not measure natural maneuverability in foot-propelled birds. Other freely swimming aquatic animals, from fish to penguins, demonstrate dramatic variation both in the sharpness and speed of turns, and in the movement strategies to control turning (Fish, 2002; Fish et al., 2003; Hui, 1985). Animals that swim like loons with a rigid body and powering swimming with the feet, including rays and turtles, demonstrate a consistent pivoting strategy. These swimmers generate drag on the turning direction side of the body by extending the feet on the inside of the turn (often called the “inboard feet”) while continuing to generate thrust using...
the outside, “outboard,” feet (Fish and Nicastro, 2003; Rivera et al., 2006). However, unlike previously studied underwater foot-propelled swimmers, loons rely solely on two, not four, limbs for propulsion. Additionally, the unusual leg anatomy of loons restricts the feet to the very caudal edge of the body (Clifton et al., 2018), which positions the feet at a long distance from the center of mass enabling efficient maneuvering (Webb, 1988). It is therefore likely loons use novel kinematic strategies to control maneuvers.

This study quantitatively evaluates swimming and turning strategies in loons for the first time. Using high-speed cameras in custom-built underwater camera cases, we film four healthy common loons freely swimming in a pool at the Tufts University Wildlife Clinic. Kinematic analysis of the body and hindlimbs during straight swimming reveals that loons power foot movement by ankle flexion and knee rotation. The feet are placed in a lateral position and appear to generate lift forces, similar to grebes. We also find that loons use head-bobbing to alternate stabilizing the head with augmenting the acceleration of the eye, likely enhancing visual localization of prey. To induce turns, loons use a combination of several strategies by modulating: (1) the speed of the outboard foot, (2) the relative timing of foot motion, and (3) particular features of each foot’s motion. Our findings provide the first evaluation of swimming in loons and reveal new mechanisms for controlling maneuvers using foot-based underwater swimming.

Materials and Methods

Swimming recordings

The unpredictability of where loons swim combined with variable water clarity hinders filming loons underwater in the wild. On the other hand, adult common loons cannot be housed in captivity for long stays since they contract an often-fatal respiratory fungal disease when under acute stress (Miller and Fowler, 2014). Common loons are listed as a species of concern in MA (321 CMR 10:00, 2010) and threatened in NH (Wildlife Action Plan, 2015), preventing the explicit capture of loons for observation in potentially life-threatening conditions. For these reasons, we filmed swimming loons at the Tufts University Wildlife Clinic (North Grafton, MA) during rehabilitation stays.

Between 2014 and 2016, four healthy loons were filmed at the Wildlife Clinic. Many of the loons brought into rehabilitation centers are not healthy enough for filming, quickly
Loon swimming and turning

succeeding to lead poisoning from fishing tackle or traumatic injuries (Sidor et al., 2003). However, some loons are admitted with minimal injuries and are quickly released back into the wild. The Tufts Wildlife Clinic primarily receives loons during fall migration. The four loons filmed in this study sustained no major injuries and were filmed on the day of release, usually during the hours just prior to release. At the time of recording, the loons weighed between 2.5 to 3.2 kg, within the normal range for adults (Johnsgard, 1987). Therefore, the data presented here accurately represent swimming by healthy loons prior to being released from the rehabilitation clinic.

Loon swimming was filmed using two high-speed cameras (NR5S1, Integrated Design Tools, Tallahassee, FL, USA) in an indoor, 3.05 m diameter pool. The cameras were placed in custom-made underwater cases using adapted scuba dive boxes and 8020 aluminum framing (Fig. S1). A wide-angle lens was attached to each camera (14mm, f/3.2, Rokinon) and focused at a distance of 1.8 m in air. The effective lens focal length increases when submerged resulting in an approximate in-focus depth of field of 1.3-2.7 m from the camera.

Specific measures were taken to minimize loon stress and loon-human interaction throughout the recording sessions in accordance with animal care protocols (Tufts IACUC G2013-103). Veterinary staff at the Wildlife Clinic removed the loon from the pool to be placed in a net-bottom cage while the camera stands and cameras were placed into the pool. The shared field-of-view of the cameras were calibrated using a custom-built submersible LED wand (30 cm length) filmed at 2 fps during at least 100 frames. As the loon was returned to the pool, length measurements of the beak, tarsometatarsus, and digits were recorded. Body mass was measured during a check-in evaluation from within 24 hours before the recording. Once returned to the pool, each loon was filmed for up to 5 hours, with regular breaks to turn off the extra, overhead halogen lights. An opaque sheet covering the netting above the pool (Fig. S1) prevented the loon from observing the researchers. Diving was often voluntary, though occasionally elicited by making a noise or moving the sheet. For each loon, 3-5 bait fish were released into the pool to elicit hunting dives. Recordings were collected using Motion Studio Software at 200 frames per second with a resolution of 2336x1728 pixels. The cameras were post-triggered and recorded a maximum of 572 frames, equivalent to 2.86 seconds. Loons were then often removed from the pool and directly prepared for transportation to be released. The field of view was calibrated
again before the set-up was dismantled. Across four individuals, we recorded 159 swimming trials.

3D motion tracking

Calibration of the cameras for each day of filming was performed to convert two-dimensional data from each camera to three-dimensional (3D) information relative to a local coordinate system. Camera calibration was performed in MATLAB (The Mathworks, Natick, MA, USA) using easyWand5 (Theriault et al., 2014). Each wand calibration included at least 500, and up to 1200, digitized frames and was calculated by estimating the focal length and principle points of the cameras. The calibrations were aligned to vertical using a large, metal calibration object placed into the pool during calibration trials.

Of 159 recorded trials, 19 provided accurate 3D analysis of stride timing, body trajectory, and hindlimb kinematics. These trials included a diversity of swimming behaviors (straight swimming vs. turning, descending in the water vs. swimming along the floor) while ensuring that the bird was in focus and that an identifiable point on the body was visible in both views (more details provided below).

Each swimming stride consists of two phases, the power stroke and recovery phase. During the power stroke the foot pushes backwards relative to the body to propel the bird forward. During the recovery stroke, the toes collapse onto each other and the foot is retracted cranially in an arc. The timing of 112 power strokes was determined by visually identifying toe abduction and adduction for each foot. Although some past studies on straight swimming define the power stroke based on the acceleration of the body (Johansson and Norberg, 2001), this measure does not account for variation between the feet, an important factor for turning. The start of the power stroke was identified as the point when the digits begin to abduct and the metatarsophalangeal (MTP) joint begins to extend. The end of the power stroke was defined as the point when the toes have mostly collapsed upon each other with the MTP joint moving cranially. A full stride was defined by the start of sequential power strokes by the same foot. Each stride was observationally classified as straight swimming or turning to the left or the right.

The body and head of the loon was tracked during portions of all 19 analyzed trials. Body tracking was possible for > 30% of the duration of 36 swimming strides and for >70% of the duration of 23 strides. Six of the 19 trials included 3D limb tracking, providing a complete
analysis of 9 strides by 4 birds. These 9 strides included three during straight swimming \((a_c < 0.75 \text{ m s}^{-1})\) see below). The six turning strides \((a_c > 0.75 \text{ m s}^{-1})\) tracked four inboard feet and two outboard feet, capturing simultaneous strokes of both feet once. Body motion was completely tracked during all 9 strides that yielded 3D limb analysis. In all, over 24,000 points were hand digitized for this study.

The body and limbs of each loon were manually tracked. Like many waterbirds, loons intensively preen and are highly sensitive to any disruption to the waterproofing of their feathers. In order to minimize stress to the birds, we could not attach markers onto the body to facilitate tracking anatomical planes of the loon. Instead, body motion was tracked most often using a feather coloration pattern at the midline of the caudal abdomen near the vent. When the vent was not visible in both cameras, either a point along the midline of the tail or a feather pattern along the back was used. The accuracy of tracking this point was always within less than a pixel. The head was tracked using either the eye or the tip of the beak. In loons, the upper hindlimb is incorporated within the abdominal body skin making the hip and knee joints invisible (Clifton et al., 2018). However, these joints remain relatively immobile in flexion/extension due to skeletal structures stabilizing both joints (Hertel and Campbell Jr, 2007; Wilcox, 1952), with most of the foot’s motion stemming from flexion and extension of the ankle. The following hindlimb landmarks were tracked for at least one limb during each of the six trials: intertarsal “ankle” joint, metatarsophalangeal joint, and distal phalanx of digits II-IV.

**Kinematics Analysis**

Power stroke time, stride time, and duty factor were determined for each foot separately throughout the trial. Power stroke time was calculated by converting the number of frames between the beginning and end of the power stroke to duration (1 frame = 5 ms). Stride duration was determined using the start of sequential power strokes since the beginning of toe abduction could be identified more accurately than toe collapse. A swimming duty factor was defined as the fraction of the stride used to power swimming, calculated as the power stride time divided by the stride time. For each of these variables, individual values were categorized as relating to straight swimming, the inboard foot during a turn, or the outboard foot during a turn.

The tracked 3D motions of the body, head, and hindlimb were smoothed and rotated relative to the forward motion and mediolateral axis of the loon. Custom MATLAB scripts applied a cubic spline (‘smoothing spline’ fit function, smoothing parameter = 0.01) to the data.
The relatively extreme smoothing parameter derives from a high frame rate relative to motion speed. Rotation matrices were defined and applied at each time-step based on trajectory-based and anatomical axes. The x-axis was defined as the travel direction of the body. The y-axis corresponds to the line connecting the left and right ankle joints, representing the mediolateral plane of the bird assuming symmetrical or limited motion of the ankles relative to the body. The z-axis was calculated as the cross product of the x- and y-axes, approximating the dorsoventral plane of the body. Loons swim with a downward anterior tilt of the body relative to the travel direction resulting in a slight offset between the z-axis and dorsoventral plane of the loon. However, the consistency of the anterior tilt among trials supported the usefulness of x-, y-, and z-axis comparisons across strides and individuals.

Average speed and turning characteristics were quantified for each stride. Previously, strides were defined for each foot using the start of power stroke. Because the feet are paddled approximately synchronously but not exactly, full-body strides were defined using the earlier power stroke of the two feet. An average speed throughout each full-body stride was calculated only if the body had been tracked for over 70% of the stride (23 strides by 4 birds). The horizontal motion of the body was analyzed to quantify the extent of turning throughout each stride while neglecting the impact of buoyant forces. For strides in which at least 30% of the stride was digitized (36 strides by 4 birds), a 2D circle was best fit to the horizontal trajectory (Taubin, 1991; Fig. S2). The radius of this circle was considered the average radius of curvature, \( r \). While past studies have used a measure of instantaneous radius of curvature, we found this measure to overestimate the turning ability of the loon due to small deviations in the loon body trajectory. Using the average radius of curvature, stride angular velocity, \( \omega \), was calculated as:

\[
\omega = \frac{u}{r}
\]

(1)

with \( u \) as the average horizontal speed throughout the stride and \( r \) the average radius of curvature from the best fit circle. From this, the centripetal acceleration acting on the loon throughout the stride, \( a_c \), is:

\[
a_c = \frac{u^2}{r}
\]

(2)

with units of m s\(^{-2}\) or expressed as multiples of gravitational acceleration, \( g \) (9.8 m s\(^{-2}\)). Together, these parameters give an approximate measure of the extent of turning throughout a stride. Strides with \( a_c > 0.75 \text{ m s}^{-2} \) were considered turns.
We statistically analyzed whether stride duration, power stroke duration, and duty factor differ if loons swim straight or turn. We tested the influence of “foot type” (straight, inboard foot, outboard foot) by fitting a linear mixed-effect model (Fit type = REML) to the data and using a Likelihood Ratio Test (MATLAB 2015b). The first model tested the influence of foot type while accounting for random effects from individual identification (Output ~ Foot + (1|Individual)). These models were repeated, binning together inboard and outboard foot data, to compare straight swimming strides to all turning strides. The Likelihood Ratio Tests were conducted using a model with the “Foot” fixed effect. We were unable to perform these analyses on foot splay (max distance between digits II and IV) due to a small sample size of tracked foot strides and relatively large anatomical variation among individual loons. To account for the influence of swimming speed on stride duration, power stroke duration, and duty factor, we repeated the linear mixed-effect modeling using an extra fixed effect (Output ~ Foot + Speed + (1|Individual)). Again, these models were performed with two separate stride groupings: straight vs. inboard vs. outboard and straight vs. all turning. The Likelihood Ratio Tests were conducted by removing the “Foot” and “Speed” effects independently. We determined significance using a cut-off of $p = 0.05$. All values are listed as the average and standard error.

**Results**

Despite swimming in a confined pool, loons exhibited a range of normal and extreme behaviors. All four filmed loons frequently dove underwater voluntarily. When a fish was released into the pool, the loon would often capture the fish within 1-2 seconds before the fish could swim down from the surface. When multiple fish were released at the same time, the loon quickly captured each individual. Most of the loons demonstrated an acute fear of humans, and would dive instantly upon hearing or seeing the researchers. One of the loons showed no fear of humans, following the researchers around the pool and actively investigating the camera cases and stands. Each loon was filmed performing escape dives as well as voluntary relaxed dives.

Within the 19 tracked trials, loons swam at body speeds ranging from 0.16 to 0.86 m s$^{-1}$, averaging 0.56 m s$^{-1}$. Our video recording frame rate (200Hz) provided a greater temporal resolution than previous studies on foot-propelled diving birds (50 Hz), enabling detailed analysis of the paddling timing and coordination. Stride duration ranged from 0.29 to 1.11 s, with an average of $0.55 \pm 0.02$ s (s.e.; Fig 1 B). Power stroke duration exhibited less variation, from
0.10 to 0.425 s, averaging 0.265 ± 0.005 s (Fig. 1A). Duty factor varied from 0.16 to 0.86, with an average of 0.51 ± 0.01. In strides where the body was digitally tracked for more than 70% of the duration (36 strides by 4 birds), speeds ranged from 0.29 to 0.89 m s\(^{-2}\), and averaged 0.54 ± 0.03 m s\(^{-1}\).

**Swimming hindlimb kinematics**

The distal hindlimb was digitally tracked for eight complete strides in six trials, including two strides with tracking of both feet, resulting in a total of nine tracked strides. Despite some variation in the kinematics among individuals and trials, all strides demonstrate qualitatively similar limb motion during the power and recovery strokes (Figs 2, 3, Movie 1). The foot (from MTP to tip of digits) begins the power stroke lateral and somewhat ventral to the abdomen. Relative to the body, the foot then arcs caudally, dorsally, and medially, ending the power stroke behind the body with the feet facing medially. This foot motion results primarily from extension of the tarsometatarsus at the intertarsal ankle, with only a small dorsal and lateral arc of the ankle relative to the body (Fig. 3, green). Note that, as depicted in Figure 3, due to concurrent forward movement of the body, the foot experiences an overall forward motion (in the travel direction) relative to still water throughout the power stroke. The foot moves opposite to the travel direction only modestly, with comparatively large excursions in the ventral-to-dorsal and lateral-to-medial directions.

Throughout the power stroke, the digits extend and abduct at their MTP joint (Fig. 3, thin, lighter blue lines). In most trials, the digits hyperextend, reaching angles greater than 180° relative to the tarsometatarsus. However, in situations where the inboard foot is used as a rudder or executes a small power stroke compared to the outboard foot, the digits only somewhat abduct and never hyperextend. As the foot reaches a position behind the loon’s body, the MTP flexes and the toes adduct, eventually collapsing onto each other and signaling the end of the power stroke.

During the recovery stroke the MTP travels in an arc cranial, medial, and slightly lateral relative to the body. The folded digits swing behind the tarsometatarsus. The ankle moves only slightly relative to the body during the recovery stroke. At the transition from recovery to power stroke, the forward-moving MTP slows down and reverses its motion to begin moving backwards relative to the body. At this point, the foot rotates from facing caudally during the recovery stroke to facing dorsally and medially during the power stroke.
Head-bobbing

In approximately one-third of the 19 tracked trials, loons exhibited head-bobbing. As their body glides forward during the recovery stroke, loons retract their neck to slow the velocity of the head relative to still water, sometimes achieving a stationary head position (Fig. 4, Movie 2). During the power stroke, the loons extend their neck, resulting in a faster acceleration of the head compared to the body. Within the 11 tracked head-bobbing strides, the head reached a maximum speed of 1.13 m s$^{-1}$ and acceleration of 7.96 m s$^{-2}$, three times faster than the body (Fig. 4). Loons did not head-bob during quick escape dives or sharp turns, but only during relatively horizontal swimming and while hunting baitfish.

Turning strategies

Since filming occurred in a relatively small circular tank, most of the tracked trials recorded loons turning. Across all 36 strides with the body tracked for at least 30% of the stride, the average stride radius of curvature, $r$, was $0.42 \pm 0.07$ m with an extreme value of $0.06$ m, or approximately 0.07 body lengths (conservatively, calculated based on a maximum body length of 0.91 m) (Table S1). The average stride angular velocity ($\omega$) was $92.4 \pm 10.9$ degrees s$^{-1}$, with an extreme of 287 degrees s$^{-1}$. The average stride centripetal acceleration ($a_c$) was $0.80 \pm 0.55$ m s$^{-2}$, with an extreme of 1.96 m s$^{-2}$ or 0.20 g.

Loons use several strategies to execute turns, including changing their body and wing positions, moving their feet at different timings, and varying factors that influence the force produced by each foot. In every observed turn, the body of the loon rolled out of the turn resulting in the ventral belly facing into the turn (Fig. 5). For many turns, loons slightly extended their wings, particularly the outer wing during tight turns (Fig. 5). During one almost 180° turn, the loon also depressed its tail throughout the maneuver.

While turning, loons paddle the inboard and outboard feet at different times. In contrast, when swimming straight loons synchronously paddle their feet, starting and stopping each foot’s power stroke at approximately the same time (Fig. 6). However, during turns, loons almost always paddled the outboard foot 0.05-0.10 s before the inboard foot (Fig. 6), representing a temporal difference of 20-40% of power stroke duration. In some cases, loons extended the toes of the inboard foot when it was held lateral to the body, allowing the inboard foot to act as a rudder. In two trials, the use of the inboard foot as a rudder was extended over repeated paddling cycles of the outboard foot (Fig. 6, bottom row).
Although loons alter the relative timing of the feet when turning, only a few stride parameters varied between straight and turning strides. Without accounting for an influence of speed, no stride parameters showed kinematic variation. However, when accounting for both average swim speed and random effects from individual variation, a few variables demonstrated significant variation (Tables S2, S3). The inboard foot used a longer power stroke compared to straight swimming strides ($p = 0.007$, Table S3, Fig. S3). Power stroke duration significantly decreased with increased stride speed for every model (Table S3). Stride duration also decreased significantly with increasing speed in all models except for when only considering straight versus outboard foot strides ($p=0.134$). Lastly, the tip of digit III on the outboard foot traveled a slightly longer, though not significantly longer, distance throughout the power stroke compared to the inboard foot (~24 cm vs. ~20 cm, Table S4), traveling at a higher average speed (1.06 vs. 0.74 m s$^{-1}$, Table S3). To summarize, (1) the stride of the inboard foot lasted longer than for straight swimming strides, (2) faster swimming loons used shorter stride times and particularly shorter power strokes, and (3) turning loons paddled the outboard foot at a faster average velocity.

Across six turning strides with the hindlimb digitally tracked, loons vary foot motion considerably (Fig. S4). Variation among inboard and outboard strides does not permit a precise description of turning kinematics, but our data reveal some consistent kinematic patterns. During straight swimming, the foot arcs caudally, dorsally, and somewhat medially relative to the body through the power stroke (Fig. 7, center). In contrast, for most turning power strokes the inboard and outboard feet reduced the dorsal component to keep the foot ventral or in line with the ankle (Figs. 7B, S4). Further, the inboard foot remained caudal to the ankle compared to straight or outboard strides where the foot sometimes reaches a lateral or even cranial position relative to the ankle (Fig. 7A). Two turning strides, one inboard foot (Fig. 7, right) and one outboard foot (Fig. S4, Trial 15), included a larger mediolateral excursion than used during straight swimming. Even though several of the turning strides resembled straight swimming motions, variability among turning strides demonstrates the ability of loons to modulate paddling kinematics and reveals a few potential turning kinematic patterns.
Discussion

The large territories of loons and their conservation status pose significant challenges for quantifying their underwater swimming kinematics. Working within a rehabilitation center, we collected detailed 3D data from 19 trials across four healthy individuals, representing both straight swimming and turns. By collecting data over three winter seasons, we were able to demonstrate consistent qualitative, as well as quantitative, findings of these exceptional underwater foot-propelled swimming birds. While observing loons in captivity may underestimate their top swimming speeds, it is unlikely that loons adjust their swimming motions and strategies for turning under confined circumstances. Therefore, we believe that our results report the first detailed analysis of natural loon swimming.

Straight swimming

During straight swimming, we record loons reaching speeds up to 0.86 m s\(^{-1}\). Studies analyzing other top foot-propelled swimming birds record faster speeds for straight swimming, 1.2 m s\(^{-1}\) in grebes (Johansson and Norberg, 2001) and 1.5-1.7 m s\(^{-1}\) in cormorants (Johansson and Norberg, 2003; Ribak et al., 2004; Watanabe et al., 2011). However, these birds were tracked swimming in the wild or through long straight corridors, unlike the comparatively small pool used in this study. We expect that the pool restricted the loons to slower speeds, and that loons likely reach faster speeds in the wild. Further, the loons accelerated up to 1.5 m s\(^{-1}\) within straight swimming strides (Table S1), which may contribute to divergence from relatively steady swimming observed in previous grebe and cormorant studies.

Under the conditions of our study, loons swim using stride frequencies within the range of other foot-propelled swimming birds, but with relatively high values for their body size. When swimming straight, loons use an average stride frequency of 2.04 Hz, similar to values found for grebes (2.50 Hz; Johansson and Norberg, 2001) and cormorants (1.10-3.25 Hz; Ribak et al., 2004; Ribak et al., 2005; Sato et al., 2007; Watanuki et al., 2005). When only comparing values for birds swimming horizontally in captivity, loons swim with faster stride frequencies than cormorants despite having a larger body mass (2.9 kg vs. 2.2 kg). Scaling patterns observed within and among aquatic swimmers (Sato et al., 2007; Sato et al., 2010) predict that larger animals should use lower stride frequencies. Therefore, despite swimming with stride frequencies within the range of other foot-propelled birds, loons use comparatively fast strides when accounting for body size. This pattern may derive from a relatively small foot area in loons.
Loon swimming and turning

Loon swimming and turning (L.C. Johansson, Lund University, personal communication) or the need to accelerate throughout the stride, however loons exhibit high stride frequencies even when experiencing low centripetal and tangential accelerations (Table S1, Trial 17).

Despite their relatively high stride frequencies, loons swim with longer power strokes compared to other foot-propelled swimming birds. The use of sequential power and recovery strokes in loons is similar to grebes but different from cormorants, which include a gliding phase with their feet held behind the body before each recovery stroke (Ribak et al., 2005). The power stroke of loons approximates 54% of the stride, lasting on averages 0.26 s during straight swimming. In comparison, the power strokes of both grebes and cormorants constitute ~25% of the stride, lasting 0.01 s and 0.16 s respectively (Johansson and Norberg, 2001; Ribak et al., 2004; 2005). Since we find that power stroke duration significantly decreases with swim speed, the difference between loons and other swimming birds observed to date could result from the comparatively slow swimming speeds of the loons in the rehabilitation pool used for this study.

Finally, loons modulate swim speed primarily by varying their power stroke duration and not stride frequency.

Loons swim by synchronously pushing their feet backward, medially and dorsally during the power stroke, and then drawing the foot forward with collapsed toes during the recovery stroke. However, this paddling is not a simple pivoting motion. The feet begin the power stroke ventral to the body with the plantar surfaces of the feet facing caudally but end with the plantar surfaces facing medially towards each other (Fig. 2). The ankle and metatarsophalangeal joints primarily function as a hinge (Stolpe, 1935), suggesting that this rotation of the foot must occur more proximally. Loons have a relatively abducted hip joint with a large antitrochanter that restricts rotation of the femur (Hertel and Campbell Jr, 2007; Wilcox, 1952), likely preventing a contribution of the hip joint to foot rotation. Instead, foot rotation likely results from rotation at the knee, as has been demonstrated in running birds (Kambic et al., 2014; Kambic et al., 2015). Loons possess an enlarged cnemial crest at the proximal end of the tibiotarsus, which almost completely encloses the anterior and posterior articular surfaces of the distal femur (Wilcox, 1952). While the cnemial crest limits flexion and extension of the knee, it permits long-axis rotation of the tibiotarsus. Grebes demonstrate a similar anatomical pattern, and also swim using long-axis foot rotation while swimming (Johansson and Norberg, 2001). Therefore, loons
probably swim by coupling flexion and extension at the ankle joint with rotation at the knee to achieve the net 3D kinematic propulsive and recovery movements of the foot.

The motion of the foot in swimming loons resembles that of grebes, suggesting that loons may also generate lift forces for propulsion. Loons (Figs. 2, 3) and grebes (Johansson and Norberg, 2001) paddle their feet lateral to the body, whereas cormorants paddle their feet ventrally underneath the body (Ribak et al., 2004). Nevertheless, all three underwater swimming species demonstrate almost no motion of the feet opposite to the travel direction relative to the surrounding water (Fig. 3). Because the feet do not substantially push water backward, propulsion cannot depend on drag forces. Instead, loons direct their feet dorsally and medially relative to still water throughout the power stroke. Consequently, this perpendicular motion relative to their travel direction likely produces drag to resist buoyancy and lift for forward propulsion. Although the foot kinematics of loons resembles that of grebes, grebes possess lobate toes that likely act as individual hydrofoils to increase lift production (Johansson and Norberg, 2000). Instead, the webbed feet of loons may enhance lift by functioning like a propeller. As the foot arcs dorsally, the surface of the foot is pitched leading with digit IV. Lift generated by the angle of attack of the foot would contribute to forward propulsion without moving backward relative to still water. This potential ‘propeller’ mechanism differs from the proposed ‘delta wing’ function for cormorant feet (Johansson and Norberg, 2003). By relying on lift instead of drag forces for propulsion, loons can produce propulsive forces at any swim speed, whereas drag-based propulsion is limited to slower speed swimming (Vogel, 2008). Thus, despite variation in whether the feet are moved ventral (cormorants) or lateral (grebes and loons) to the body, three independent lineages of foot-propelled swimming birds indicate the probable use of lift-based propulsion.

Contrary to previous findings (Jiménez Ortega, 2005), we observed that swimming loons bob their head, likely to enhance their vision. Dozens of bird species across the avian phylogeny exhibit head-bobbing while walking, flying, or swimming (Jiménez Ortega, 2005; Ros and Biewener, 2017; Wallman and Letelier, 1993). Head-bobbing consists of thrust and hold phases, allowing head (and eye) motion to be dissociated from motion of the body (Necker, 2007). The thrust phase accelerates the head (and eyes) forward relative to the body’s motion. The hold phase then allows the head (and eyes) to be held briefly in place, stabilizing the bird’s gaze. Head-bobbing has been argued to improve vision by increasing depth perception through
Loon swimming and turning

parallax during the thrust phase, followed by pattern and motion identification during the hold phase (Necker, 2007; Wallman and Letelier, 1993). Prior to our findings, loons were reported not to use head-bobbing (Jiménez Ortega, 2005). Yet, we find clear evidence of head-bobbing when loons swim underwater, accelerating their head (and eyes) more than three times faster than their body (Fig. 4, Movie 2). The use of head-bobbing while voluntarily diving but not during escape dives suggests its possible use for localizing and pursuing prey. Two other foot-propelled diving birds, grebes (Gunji et al., 2013) and mergansers (Lindroth and Bergstöm, 1959), have also been observed to head-bob. Our observation of head-bobbing in loons suggests that this behavior may be broadly representative of foot-propelled diving birds, including groups previously considered not to head-bob, such as cormorants. Because head-bobbing likely enhances vision for hunting prey, it may represent an important function of the comparatively long necks of foot-propelled diving birds.

Turning strategies

Previous studies of foot-propelled swimming birds have focused on swimming through a tunnel or navigating a single vertical obstacle (Johansson and Norberg, 2001; Ribak et al., 2004; 2008). Our study is the first to analyze turning maneuverability of a freely diving foot-propelled bird. Although our findings may not represent the extreme abilities of loons to turn when swimming in the wild due to the confined nature of the swimming pool, we were able to observe maneuvers that likely approach high-level loon turning performance.

Compared to other studied underwater swimmers, the loons in this study execute tight turns but at slow speeds. The minimum radius of curvature observed (0.06 m or 0.07 body lengths (L); Fig. S2), was significantly smaller than other diving animals, including sea lions (0.16 m or 0.09 L), penguins (0.14 m or 0.24 L), and cetaceans (0.19 m or 0.15 L) (Fish, 2002; Fish et al., 2003; Hui, 1985). Even so, as a measure of maneuverability, turning curvature does not alone characterize turning performance. The angular rate of change in heading direction serves as a measure of agility, and also influences the ability to capture prey. Loons execute turns at up to 287 degrees s\(^{-1}\), more slowly than the maximum rates in sea lions (690 degrees s\(^{-1}\)) and penguins (576 degrees s\(^{-1}\)), but comparable to dolphins (Fish, 2002), turtles (Rivera et al., 2006) and some teleost fish (average 140-180 degrees s\(^{-1}\); Webb and Fairchild, 2001). However, due to the relatively slow swimming speeds that we observed, loons turn with a centripetal acceleration (maximum of 0.2 g) much lower than sea lions (5.13 g) or cetaceans (3.56 g). The observation of
loons in this study performing sharp but slow turns compared with other underwater hunters may highlight differences in hunting strategy. Sea lions, penguins, and cetaceans typically hunt in open water requiring them to out-chase their prey. In contrast, loons primarily search for prey on the ocean or lake floor, often probing along rocks then quickly snatching any flushed animals (Johnsgard, 1987). This strategy relies on maneuvering in relatively tight spaces, but at slow speeds until quickly accelerating to capture a fish at close range. Additionally, a potentially important difference between loons and all previously studied turning animals is their long and flexible neck. Limitation to their body’s turning ability may not adequately reflect the effective capacity for loons to rotate their head for prey capture. Hunting strategies of loons or other long-necked diving birds has not been quantitatively studied, suggesting an important future direction of this work.

To turn underwater, loons must create a force differential between the sides of their body or redirect the force produced by the feet to produce a swimming torque that rotates the body. There are three main ways that this can be achieved. First, loons could produce stronger propulsive forces on the outboard side relative to the inboard side of the turn. Second, loons can vary the relative timing of force production by each foot. Third, loons could control a turn by redirecting the propulsive forces by altering individual motion of the feet. The following section examines evidence for these turning strategies.

To alter the force produced on each side of the body, loons increase the speed of the outboard relative to the inboard foot. The force each foot produces during the power stroke depends on foot area (abduction of the digits) and speed squared (influenced by both duration of the power stroke and distance traveled by the foot). Due to individual variation and the limited number of turning trials with the foot tracked, no significant evidence was found for more abducted digits on the outboard versus inboard foot. However, loons appear to alter the speed of the outboard foot during the power stroke, modifying both duration and distance relative to still water. Accounting for variation due to swim speed, the power stroke of the outboard foot is significantly shorter than that for the inboard foot during turns (Table S2). The tip of digit III of the outboard foot travels a slightly longer distance throughout the power stroke (not significant), but moves at a significantly faster speed. In more extreme cases of turning, loons dramatically alter inboard versus outboard forces by only paddling the outboard foot or by inducing a
Loon swimming and turning

backwards drag-based force using the inboard foot as a rudder. These strategies result in a net force acting to rotationally accelerate the loon’s body into the turn.

Loons were also observed to paddle the outboard foot before the inboard foot to help initiate and maintain turning. Paddling the outboard foot first amplifies the temporal difference in force between outboard and inboard sides during the early part of the turn. Any force produced by the outboard foot is transmitted to the body at a point lateral to the bird’s center of mass. Without a counteracting force from the inboard foot, the thrust from the outboard foot produces a yaw torque (a rotation around the dorsoventral axis of the bird) into the turn. As the body rotates, the center of mass moves towards the inboard foot, reducing and potentially inverting the yaw moment arm of the inboard foot. The force from the delayed inboard power stroke would then act behind or even outside of the center of mass to sustain the turn.

Our observation that the loon’s body rolls outward from the turn is a likely consequence of the temporal offset and differential forces produced by the outboard relative to inboard foot. Loons experience upward buoyant forces at shallow depths, as evidenced by their tendency to ascend passively. In order to resist buoyancy, each foot must produce a downward force component. Because loons swim with a slight head-down tilt of the body, their center of mass lies below their feet. When the outboard foot paddles earlier and with a greater force than the inboard foot, the downward vertical component of its force acts on the body above and lateral to the center of mass, producing an upward pitch moment and an outward roll moment. As a result, the ventral belly of the loon rotates in toward the turn. Any downward force from the inboard foot will oppose this roll and stabilize the body. In some cases, loons were observed to slightly extend the outboard wing, which would also help to stabilize the body about its roll axis. Many underwater swimmers, including most cetaceans and sea lions, roll into turns to exploit back flexion to increase maneuverability (Fish, 2002; Fish et al., 2003). However, beluga whales and penguins roll out of turns like loons (Fish, 2002; Hui, 1985). Previously it has been suggested that the body of foot-propelled birds generates a downward-directed lift, which aids turning when the body rolls outward (Johansson, 2002). This benefit of rolling outwards during turns likely applies to loons, and may extend to other swimmers that produce turning forces behind the center of mass.

Turning loons also adjust the 3D motion of their feet to reduce forces that would oppose the turn. While turning, both feet demonstrate a decreased ventral to dorsal component of motion
compared to straight swimming (Figs. 7, S4). With the body rolled away from the turn, any
ventrally-directed force will point into the turn. Because the forces produced by the feet act on
the body behind the center of mass, these ventral forces would induce adverse yaw moments that
resist the turn. Reducing dorsoventral motion of the feet during turns therefore serves to limit
forces that resist turning.

Conclusions
Loons rely on swimming for hunting, mating, and predator evasion. As one of several
independent lineages of adept foot-propelled swimming birds, loons provide critical insight into
the physical demands, control strategies, and evolutionary drivers of swimming. We find that
loon swimming resembles that of grebes and likely depends on lift generation for propulsion.
Loons modulate the duration of the power stroke when varying swim speed and use head-
bobbing to enhance underwater vision. Our findings suggest that loons produce propulsive
swimming forces convergently to grebe strategies, but diverge from cormorants, which retain the
ability to walk on land. As the first study to analyze turning in freely swimming foot-propelled
birds, we find that loons roll outward from turns and use a combination of paddling mechanisms
while turning. Loons increase the speed of the outboard foot, shift the timing of the outboard
power stroke to before that of the inboard foot, and vary the individual motions of the inboard
versus outboard feet to turn while swimming underwater. These results may provide inspiration
for the design and control of swimming robots, with further application to paddling sports.

List of Abbreviations

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<tbody>
<tr>
<td>$a_c$</td>
<td>average horizontal centripetal acceleration acting throughout a stride</td>
</tr>
<tr>
<td>$g$</td>
<td>gravitational acceleration, $9.80655 \text{ m s}^{-2}$</td>
</tr>
<tr>
<td>MTP</td>
<td>metatarsophalangeal joint</td>
</tr>
<tr>
<td>$r$</td>
<td>average horizontal radius of curvature throughout a stride</td>
</tr>
<tr>
<td>TMT</td>
<td>tarsometatarsus</td>
</tr>
<tr>
<td>$u$</td>
<td>average horizontal velocity throughout a stride</td>
</tr>
<tr>
<td>$\omega$</td>
<td>average angular velocity throughout a stride</td>
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Competing interests

The authors declare no competing or financial interests.

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Author Contributions

GTC collected data, performed experiments, analyzed data, and prepared the manuscript. AAB provided guidance throughout the study and assisted with writing.
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Loon swimming and turning


**Ribak, G., Weihs, D. and Arad, Z.** (2008). Consequences of buoyancy to the maneuvering capabilities of a foot-propelled aquatic predator, the great cormorant (Phalcrocorax carbo
Loon swimming and turning


Figure 1. Descriptive stride parameters of straight and turning swimming. Data from 112 strides in 19 trials across four loons showing values for all strides (black), straight swimming strides (dark grey), inboard foot of turning strides (medium grey), and outboard foot of turning strides (light grey). Violin plots (vertically-mirrored histograms) show (A) power stroke time, (B) stride time, (C) duty factor, and (D) body speed during strides. Data for stride speed is combined for inboard and outboard feet as turn data (medium grey). The width of each bin represents the number of data points, with values consistent across all panels. Dashed lines show the mean of each distribution. Numbers at the left list the total number of strides depicted in each plot.

Figure 2. Lateral view of loon power stroke during straight swimming. Each image is cropped from one camera’s full field of view. The cropped area does not change among panels, representing loon motion relative to still water. Loons propel the body forward by extending the intertarsal ankle joints. Each foot travels in a lateral, backwards arc relative to the body due to extension at the intertarsal ankle joint. Throughout the power stroke, the digits abduct and extend at the MTP joints. The power stroke ends as the ankle begins to flex, bringing the MTP joint forward and collapsing the digits onto each other. For this stride, the power stroke lasted 0.24 s. The circles and lines in the 4th panel denoting anatomical landmarks correspond to the colors used in Figures 3 and 7.

Figure 3. Right foot motion during straight swimming relative to still water rotated in reference to the loon. The traces show tracked motion relative to still water from a recovery stroke (thin lines), power stroke (thick lines), then another recovery stroke of a loon swimming in a straight trajectory. The 3D data were rotated to be in reference to the travel direction (x-axis)
and mediolateral plane (A y-axis), with the 3rd coordinate axis representing a tilted dorsoventral plane (B y-axis). (A) View of the right limb from above the loon showing the body (dark gray), intertarsal ankle (green), metatarsophalangeal joint (MTP, red), and tip of digit III (turquoise). (B) View of the right limb from the right side of the loon. The bold and lighter shade traces represent the power stroke. The thin gray lines represent the two skeletal elements. Proximally, the tarsometatarsus connects the ankle to the MTP joint. Distally, digit III connects the MTP joint to the tip of digit III. Thin, lighter blue lines connect the tip of digit III to the tips of digit II and IV. Lines represent every 3rd frame (0.015 s). Both panels scaled to 10 cm scale bar.

Figure 4. Body and head speed of a head-bobbing loon. Bold traces show the body (black) and head (gray) speed of a common loon swimming underwater throughout time (x-axis). Gaps in the traces represent regions where the view of the tracked feature was obstructed. Crosshatched panels depict the timing of the right and left power strokes, as determined by observing foot motion. Average acceleration was calculated as the change in speed over change in time from the lower speed to the highest speed within a stride. Head-bobbing allows loons to stabilize the head, and likely their gaze, during late recovery stroke. During early power stroke as the body accelerates, loons extend the head reaching accelerations over three times faster than the body.

Figure 5. Observed turning strategies of loons. Still shot frames from three trials depict strategies that loons use to turn. “L” or “R” in the bottom right corner of each pane denotes the turn direction. (A) A loon makes a left turn using its inner, left foot as a rudder and rolling its body away from the turn. (B) Turning to the right, a loon varies the timing of its feet. The
outboard, left foot began its power stroke earlier and has reached a point behind the loon while
the inboard, right foot has only traveled halfway through its power stroke. Though difficult to
view from this camera angle, the loon body rolls away from the turn. (C) A loon makes a sharp
turn to the left by varying the timing of its feet, extending its outboard wing, and depressing its
tail. The body of the loon rolls away from the turn.

**Figure 6. Power stroke timing of feet during straight swimming and turns.** The timing of
power strokes was tracked in several trials. Lines represent power strokes with gaps indicating
recovery strokes of each foot throughout time (x-axis). Loons generally swim with both feet
paddling synchronously as seen in the straight swimming trials (black). However, during turns,
the outboard foot (light grey) consistently begins its power stroke slightly before the inboard foot
(dark grey). The trials displayed here show data from both left and right turns, normalized for
inboard and outboard feet. In some cases (shown in bottom trial), the inboard foot was held
laterally in a mid-power stroke position, serving as a rudder, while the outboard foot was paddled
several times.

**Figure 7. Right foot motion with respect to the body during straight swimming and
turning.** The traces show tracked motion relative to the body from a full stride, including power
stroke (bold) and recovery stroke (thin). Strides from three trials show the foot on the outside of
the turn (left, “outboard”), the foot while swimming in a straight trajectory (center), and the foot
on the inside of the turn (right, “inboard”). The 3D data were rotated to be in reference to the
travel direction (x-axis), mediolateral plane (A, y-axis), and dorsoventral plane (B, y-axis) and
translated to account for body motion (Note this is a different kinematics representation than Fig.
3, in which the foot kinematics are in relation to the water and not the body’s motion). (A) View of the right limb from above the loon showing the intertarsal ankle joint (green), metatarsophalangeal joint (MTP, red), and tip of digit III (turquoise). Thin, lighter turquoise lines connect the tip of digit III to the tips of digit II and IV every 3rd frame (0.015 s). (B) View of the right limb from the right side of the loon. All panels scaled to 15 cm scale bar. During the stride for the outboard foot, the loon turned with a radius of curvature (r) of 0.09 m and angular velocity (ω) of 247° s⁻¹. The turn depicted for the inboard foot stride had an r of 0.49 m and ω = 75° s⁻¹.
A. View from above

B. View from right side

Power stroke: 0.27 s
Recovery stroke: 0.16 s

Dorsal
Ventral
Lateral
Medial

I
II
III
IV

Movement direction

Travel direction

10 cm
### Loon Speeds and Accelerations

**Speed (m/s)**

<table>
<thead>
<tr>
<th>Time (s)</th>
<th>Head</th>
<th>Body</th>
</tr>
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<tbody>
<tr>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>0.5</td>
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<td>1.0</td>
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<tr>
<td>1.5</td>
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<td>0.0</td>
</tr>
<tr>
<td>2.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

**Acceleration (m/s²)**

- **Head**
  - 0.0: 1.22
  - 0.5: 3.10
  - 1.0: 2.36
  - 1.5: 1.89

- **Body**
  - 0.0: 2.10
  - 0.5: 5.86
  - 1.0: 7.96
  - 1.5: 6.49

**Power Strokes**

- **Right foot**
- **Left foot**

**Graph Description**

- **X-axis**: Time (s)
- **Y-axis**: Speed (m/s)
- **Legend**: Acceleration and Speed curves for Head and Body.
A. Inboard foot as rudder

B. Differential timing of feet

C. Body roll away from turn; tail flexion; wing extended

A. B. C.

L R L
A. View from above

outboard foot

stright trial

inboard foot

medial

lateral

B. View from right side

dorsal

ventral

travel direction

15 cm

intertarsal ankle

metatarsophalangeal joint

digit III

movement direction