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Amanda Marie Palecek

Clemson University, apalece@g.clemson.edu

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THE INFLUENCE OF WATER DEPTH ON THE LOCOMOTOR KINEMATICS OF
THE CHILEAN FLAMINGO (*PHOENICOPTERUS CHILENSIS*)

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Biological Sciences

by
Amanda Marie Palecek
December 2019

Accepted by:
Dr. Richard Blob, Committee Chair
Dr. Samantha Price
Dr. John Desjardins
Dr. Miriam Ashley-Ross

ABSTRACT

Vertebrates exhibit a diverse range of locomotor modes and associated morphological structures. Although many vertebrates can be classified as using distinct aquatic or terrestrial locomotor behaviors, several species use a terrestrial mode of locomotion while only partly submerged in aquatic environments, a behavior called wading. Wading can be observed in a variety of taxa including amphibians, reptiles, mammals, and birds.

Although there are over 100 species of wading birds, quantitative measurements of avian wading kinematics have not been performed. To address the lack of comparative studies on avian wading kinematics, video footage of *Phoenicopterus chilensis* (Chilean flamingo) was collected and analyzed for several kinematic variables during walking on land and wading through increasing depths of water. Step height increased as water depth increased, indicating exaggerated hindlimb movements in deeper waters. Minimum ankle angle, and tibiotarsal angle to the horizontal, decreased in deep waters, indicating greater folding together of the tibiotarsus and tarsometatarsus that likely reduced drag induced by contact between water and the limb. In addition, the minimum angle of the head and the minimum distance between the head and body both increased with increasing water depth, potentially reflecting changes in mass distribution allowed by the increased buoyancy afforded by deeper water. These results demonstrate that wading birds make several kinematic adjustments as they move through increasing depths of water, potentially helping them accommodate changes in both drag and buoyancy across habitat gradients.

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INTRODUCTION

The environment in which an animal lives can profoundly affect its mode of locomotion. For example, aquatic environments can expose animals to considerably different forces than they would experience on land, where they are surrounded by air. Many of these differences relate to the buoyancy of animals and the consequent reduction of the weight that their limbs must support when in water (Zug, 1971; Ashley-Ross et al., 2009). Moreover, for animals moving at comparable speeds, water also imposes more drag than moving through air (Vogel, 2003). Despite such differences in functional requirements, many animals make use of both aquatic and terrestrial habitats. To move through these different regimes, many species will change their locomotor behavior, switching from walking on land to swimming while in water. Such behavioral changes can lead to changes in limb and body movements, muscle activation, and skeletal loading (Gatesy & Biewener, 1991; Gillis & Blob, 2001; Rivera & Blob, 2010; Andrada et al., 2013; Andrada et al., 2015; Young & Blob, 2015).

Although locomotor changes between water and land are substantial for some vertebrate species, a diverse range of tetrapods do not make dramatic changes in locomotor mode between habitats and, instead, use walking movements both in water and on land. Such species include several taxa of turtles and salamanders that commonly walk while fully submerged (Zug, 1971; Willey & Blob, 2004; Ashley-Ross & Bechtel 2004; Ashley-Ross et al., 2009), thereby incurring considerable effects from buoyancy as the entire body is underwater during stepping. In contrast, a diverse range of animals that includes some birds, primates, and large mammals, commonly engage in wading

behaviors, in which the limbs move through water, but the feet contact the submerged substrate and the body is supported partly or entirely above the water. Wading species may experience little buoyancy but, instead, may incur drag on the limbs from moving through water while still being required to support the weight of the body.

Birds are one of the vertebrate clades that most commonly exhibit wading behaviors. Many lineages of wading birds such as cranes, herons, ibis, and flamingos, spend most of their lives in or around shallow water, and walk through such water while seeking resources such as prey or nesting sites (Hartman, 1961; Powell, 1987; Velasquez, 1992; Pickens, 2017). Previous studies have focused on different aspects of terrestrial avian bipedalism and the challenges that birds face while moving over the ground (Gatesy & Biewener, 1991; Daley, 2006; Andrada & Blickhan, 2013; Andrada, 2015; Barringham et al., 2019). However, even for species that regularly use wading behaviors, there is little information on how wading through water influences avian locomotion. Do birds change the way that they move their limbs to accommodate the additional drag that deep waters impose?

Motivated in part by potential therapeutic and healthcare implications (Haupenthal et al., 2010), previous studies of limb kinematics during wading have focused primarily on quadrupeds (Barnicoat & Wills, 2016) or on human bipeds (Kuliukas, 2001; Barela et al., 2005). There are several mechanical differences between bipedalism versus quadrupedalism (Nakatsuka, 2003), as well as between avian bipedalism and human bipedalism (Alexander, 2004). Whereas human bipedalism, which utilizes a plantigrade foot posture, is suggested to be stiffer and more energy efficient,

avian bipedalism, which utilizes a digitigrade foot posture, is regarded as more compliant and stable (Gatesy & Biewener, 1991; Hugel et al., 2003). Thus, previous studies may not provide a sufficient basis to predict the impacts of wading on the locomotion of the diverse avian lineage. Moreover, as birds move through different depths of water, greater contrasts from terrestrial locomotion could emerge. Given the potential implications of the physical features of water for limb-based locomotion, direct measurement is needed to evaluate the impact of aquatic environments on avian walking.

Flamingos are an advantageous group in which to study the locomotor effects of wading through different water depths. Flamingos spend most of their lives in or near shallow water and, although they can swim in deep water, they will typically wade through the water while feeding (Bildstein, 1993; Caziani, 2007). Flamingos are also large and brightly colored compared to most other wading birds, facilitating the filming and tracking of landmarks on their body and legs. Moreover, recent anatomical studies on the mechanics of the standing flamingo leg provide a context for locomotor support that may be less available for other species (Chang & Ting, 2017).

A variety of kinematic changes are expected to occur when transitioning between terrestrial locomotion to wading through various depths of water (Coughlin & Fish, 2009). First, step height is predicted to increase as water depth increases, helping to avoid dragging the limbs through shallow water. In turn, this will correspond with a decreased minimum angle of the ankle, reflecting folding of the limb that can raise the foot above the water. In especially deep water, step height may eventually decrease and ankle angle increase, as it could become kinematically awkward and unstable to continue elevating

the limbs above deep water. Due to increased step heights in shallow waters, stride length is likely to decrease, resulting in shorter but higher steps. Such changes could help to increase stability, despite taking high steps in shallow water (Espy et al., 2010). However, stride length may increase again as water depth increases and step height eventually lowers. In addition, stride velocity should decrease as water depth increases, due to the energetic costs associated with fast wading and moving through a viscous medium (Owen, 2006; Halsey et al., 2014).

Beyond changes in limb movements, changes in other patterns of body motion may also occur. Flamingos do not typically display the head bobbing seen in some other species of birds (Necker, 2007; Hancock, 2013); however, many quadrupeds exhibit changes in the position of their head and neck relative to the body in relation to changes in speed, direction, or incline, helping to stabilize the body and improve visual fixation (Mulayara et al., 2002; Menz, 2003). I predict that, in shallow water, the head will be held at an angle close to or beyond vertical (90°), with the beak posterior to the eye and the distance between the head and body minimized, because moving through shallow water with increased drag and minimal effects of buoyancy may require flamingos to hold their extremities closer to their center of mass to remain stable. In contrast, head angles will be lower and the distance between the head and body may increase in terrestrial and deep-water strides, as greater buoyancy in deep water (and reduced drag in the terrestrial strides) could allow for greater freedom in head position.

Here, I compared the limb and body kinematics of Chilean flamingos walking through varying depths of water. This work aims to improve our understanding of the

kinematics of avian bipeds while moving through a challenging environment - wading in water compared to walking through air on land. These data could be valuable for further understanding of water-to-land transitions (Young et al., 2017) or better understanding of the relationships between hindlimb kinematic behaviors across avian phylogeny (Thomas et al., 2004; Barbosa and Moreno, 2008). Additionally, this work could potentially provide a model for the design of bioinspired vehicles capable of stable and energy efficient locomotion through a variety of habitats (Hugel et al., 2003). The results also may have implications for the design of zoological enclosures that could help ensure that captive wading birds are kept in areas that limit locomotor difficulties.

MATERIALS AND METHODS

Experimental animals

Five adult Chilean flamingos (*Phoenicopterus chilensis*) were housed and cared for by the Greenville Zoo staff (Greenville, SC). Flamingos were fed commercial flamingo pellet feed and had constant access to water. Two-hour filming sessions occurred between August 2018 and September 2019; with at least a week between filming sessions. All procedures were approved by the Clemson University IACUC (AUP 2017-078) and the Greenville Zoo veterinary staff (Zoo Veterinarian Nikolay Kapustin).

Measurement of walking and wading kinematics

All filming was conducted in the flamingo enclosure, which included a still water lagoon surrounded by dry land (*Fig. 1*). Videos were captured using three GoPro Hero 4 cameras (GoPro, Inc, San Mateo, CA) placed in a triangular formation (*Fig. 2*). Because animals were not allowed to be handled or marked, zookeepers guided all five birds to walk or wade in front of the camera array. Individual birds were identified based on unique body markings. A locomotor cycle was defined to begin when the hindlimb furthest from the camera array was fully protracted, and to end at the next point of full protraction for the same limb (N= 145; ~30 trials per bird). Strides from either the left or right leg were used, depending on the direction a bird was moving past the cameras.



Figure 1: Photograph of the enclosure in which all filming was conducted. The enclosure included a lagoon that graded from shallow to deeper waters for filming aquatic strides, and a dry mud bank for filming terrestrial strides.



Figure 2: Still image of flamingos walking in front of the camera array used for video filming.

Videos from all three cameras were captured simultaneously, and manually synchronized using a light flash visible in all three cameras. Fisheye distortion from the GoPro cameras was corrected in Adobe Premiere Pro CC 2018 (Adobe Systems, Inc., San Jose, CA). A calibration object of known dimensions was filmed prior to each video session, allowing videos from multiple two-dimensional views to be coordinated to reconstruct bird movements in three dimensions, using routines available through DLTDataViewer5 software (Hedrick, 2008). To measure bird movements, DLTDataViewer5 (Hedrick, 2008) was also used to track ten points on their bodies. These points included the eye, tip of the beak, the dorsal base of the neck where it meets the body, the tip of the tail, the margin of the tibiotarsus closest to the camera where it meets body feathers, the middle of the ankle of the leg closest to the camera, the metatarso-phalangeal joint of the leg closest to the camera, the tip of the longest digit on the leg closest to the camera, the distal edge of the ankle on the leg furthest from the camera, and, in shallow water and on land, the metatarso-phalangeal joint of the leg furthest from the camera (*Fig. 3*). In deep water that covered the ankle joint, these points included the eye, tip of the beak, the dorsal base of the neck and body, the tip of the tail, the proximal margin of the near and far tibiotarsi where they met body feathers, the ankles of both legs when visible, and the point where each leg met the water.

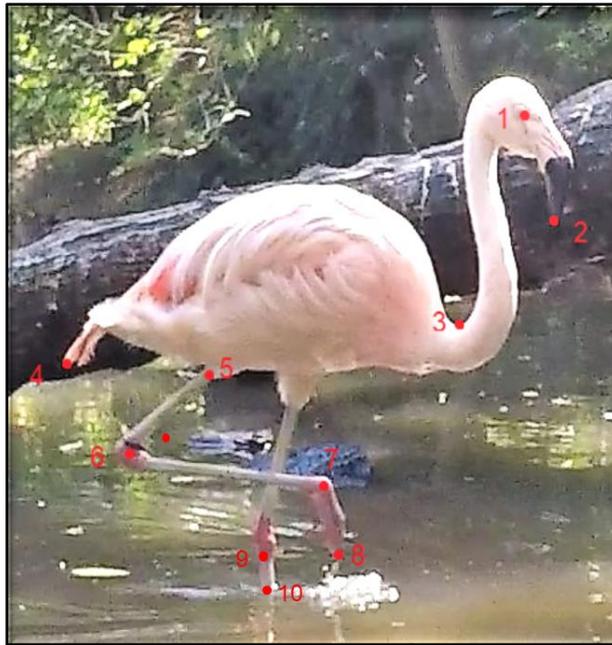


Figure 3: Illustration of 10 anatomical landmarks on flamingos that were used to track wading kinematics on videos.

Tracked marker data were processed through custom Matlab (Mathworks, Natick, MA) routines to calculate kinematic variables from each trial. These variables included angles of the hindlimb segments and joints, head extension and flexion angles, the maximum and minimum distance of the head from the body, step height, stride length, and stride velocity. To facilitate comparisons of kinematic profiles for locomotor cycles of different absolute durations, the calculated variables were processed through a quintic spline (Walker, 1998) to smooth and interpolate kinematic variables to 101 values. These values represent 0-100% of the stride cycle, where 0 indicates full protraction of the hindlimb furthest from the camera.

Statistical Analysis

Variables based on length measurements of the birds (e.g., step height, stride length, and velocity) were normalized by the head length of each bird (measured as the distance between the eye and the tip of the beak) prior to analysis. This normalization helped to account for size differences between individuals. Similarly, water depth measurements were also normalized across the five birds to reflect the maximum percentage of the leg that was covered by water during the stride. Coverage to the ankle was considered 100%, and coverage to the juncture between the tibiotarsus and the body feathers was considered 200%. Thus, shallow water depths that did not reach the ankle ranged between 0-99%, and deep water depths that submerged the ankle and placed part of the tibiotarsus under water ranged between 100%-200%.

All statistical analyses were performed in Statview 5.0 (SAS Institute Inc., Cary, NC) for Macintosh or R (R Core Team, 2013). Regressions were used to test for changes in step height, stride length, velocity, the distance between the head and body, and angles of the head and limbs across increasing depths of water. Individual birds were included in analyses as random effects, but these effects were minimal, so individual effects were ultimately excluded from the analyses that were the primary focus of interpretation.

RESULTS

Regressions indicated that several kinematic variables showed significant changes associated with increasing water depth (Table 1). However, for other variables clear relationships with water depth were not evident.

Stride Velocity and Length

Neither stride velocity (ANOVA; $P=0.2548$, $F=1.308$, $R^2=0.0093$) nor stride length (ANOVA; $P=0.5843$, $F=0.3008$, $R^2=0.0649$) changed significantly with increasing water depth (Table 1, Figs. 4, 5).

Table 1. ANOVA results for regressions of kinematic variables against water depth across all five flamingos (N=145 strides unless noted); *=significant at $P<0.05$, **=significant at $P<0.005$, *=significant at $P<0.0005$).**

Variable	F- Value	R ² - Value	P- Value
Stride Velocity	1.308	0.0093	0.2548
Stride Length	0.3008	0.0022	0.5843
Step Height	9.649	0.0649	0.0023**
Min Ankle Angle (N=115)	21.14	0.1612	<0.0001***
Max Tibiotarsal Angle	0.55	0.0039	0.4596
Min Tibiotarsal Angle	26.27	0.1589	<0.0001***
Max Head Angle	0.0154	0.0001	0.9012
Min Head Angle	7.218	0.0493	0.0081**
Max Head-Body Distance	0.3292	0.0023	0.567
Min Head-Body Distance	4.796	0.0333	0.03019*

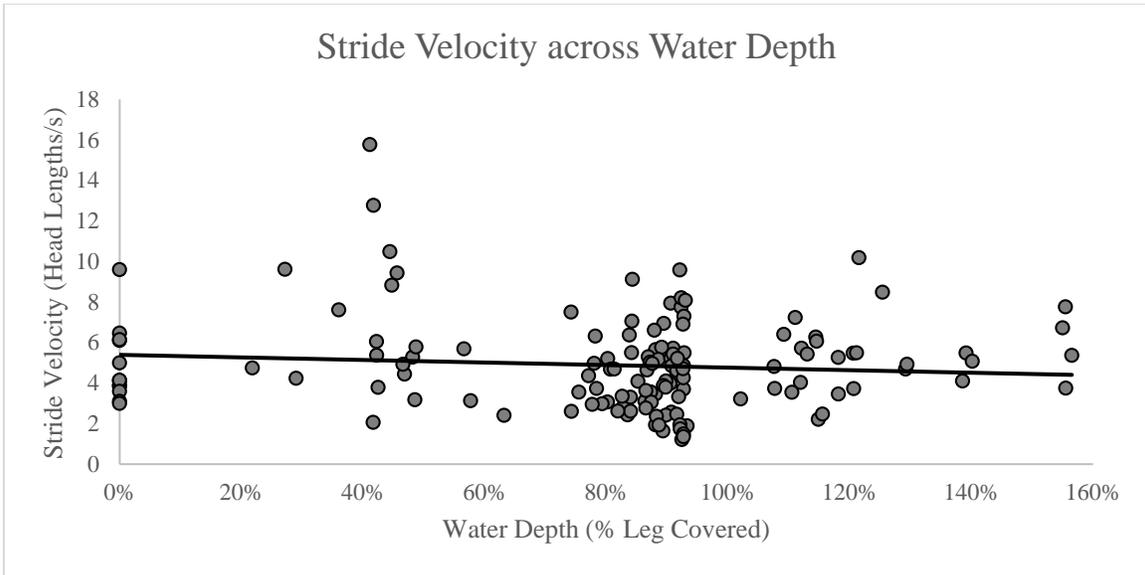


Figure 4: Stride velocity for flamingos (pooled $N=5$ animals, 145 strides) regressed on water depth. There was not a significant trend for flamingos to take faster or slower strides in deeper water.

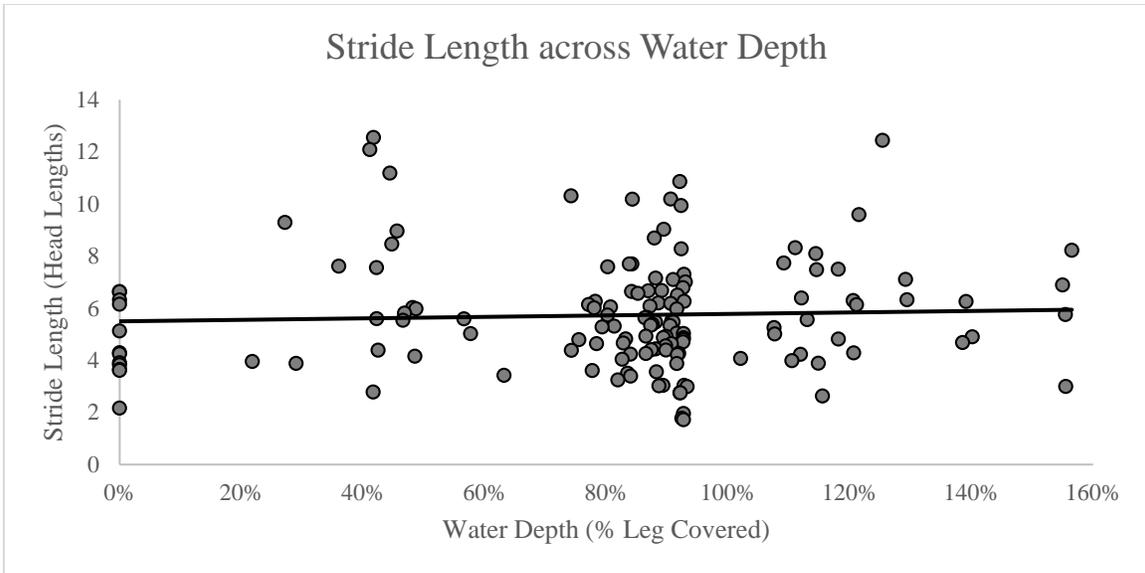


Figure 5: Stride length for flamingos (pooled $N=5$, 145 strides) regressed on water depth. Stride length was not correlated with water depth.

Step Height

Step height was characterized as the minimum vertical distance between the ankle and the body, normalized by head length. Thus, higher step heights had smaller values (i.e. smaller distance between the ankle and the body). Step height had a significant but weak relationship with water depth (ANOVA; $P=0.0023$, $F=9.649$, $R^2=-0.0649$), in which flamingos raised their ankles closer to the body with increasing water depth (Table 1, Figure 6).

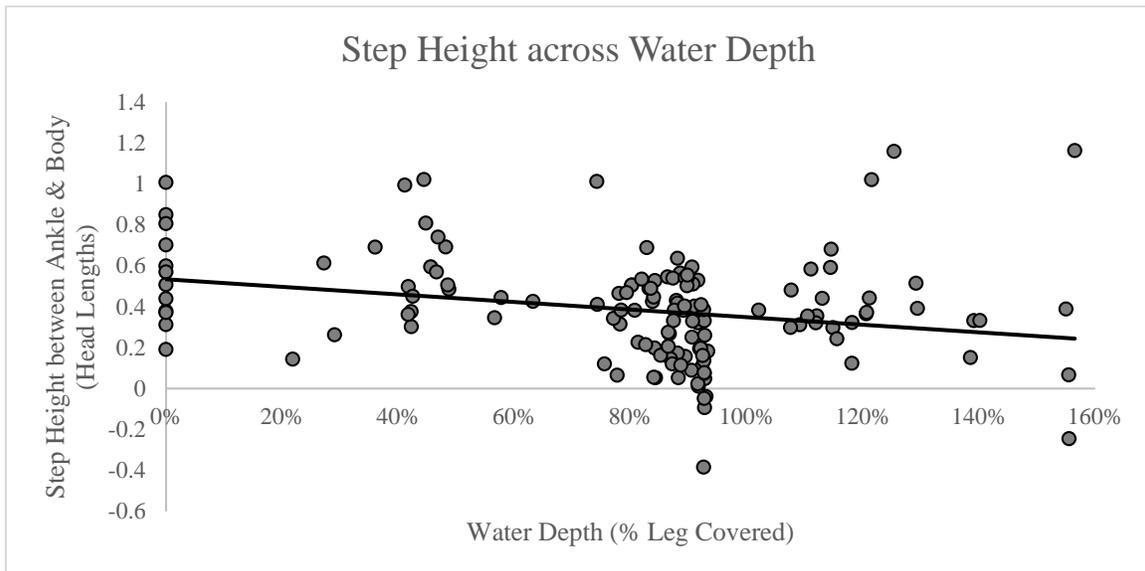


Figure 6: Step height (normalized by head length) for flamingos (pooled $N=5$ animals, 145 strides) regressed on water depth. Note that because step height was evaluated as the minimum vertical distance between the ankle and the body, larger positive values of step height indicate greater ankle-to-body distances, or lower step heights; moreover, negative values indicate that the ankle raises above the body. Step height had a significant relationship with water depth, where distance between the ankle and body decreased as water depth increased.

Ankle Angle

The ankle was extended to a nearly straight position at the start of each stride, then flexed to an approximately right angle by midstep before extending again at the end of the stride (*Fig. 7*). The minimum angle of ankle flexion could only be calculated for strides that had the ankle and tarsometatarsus visible at all phases of the stride, so strides in deep water were excluded from this analysis (n=115). Minimum ankle flexion angle decreased significantly as water depth increased (ANOVA; $P < 0.0001$, $F = 21.14$, $R^2 = 0.1612$), indicating that the leg folds more as water depth increases. Such folding could reflect an effort to raise more of the leg out of the water as it becomes deeper, helping to reduce drag. The maximum angle of the ankle did not change significantly with water depth, with all steps reaching a nearly straight angle at the beginning and end of each cycle (*Fig. 7*).

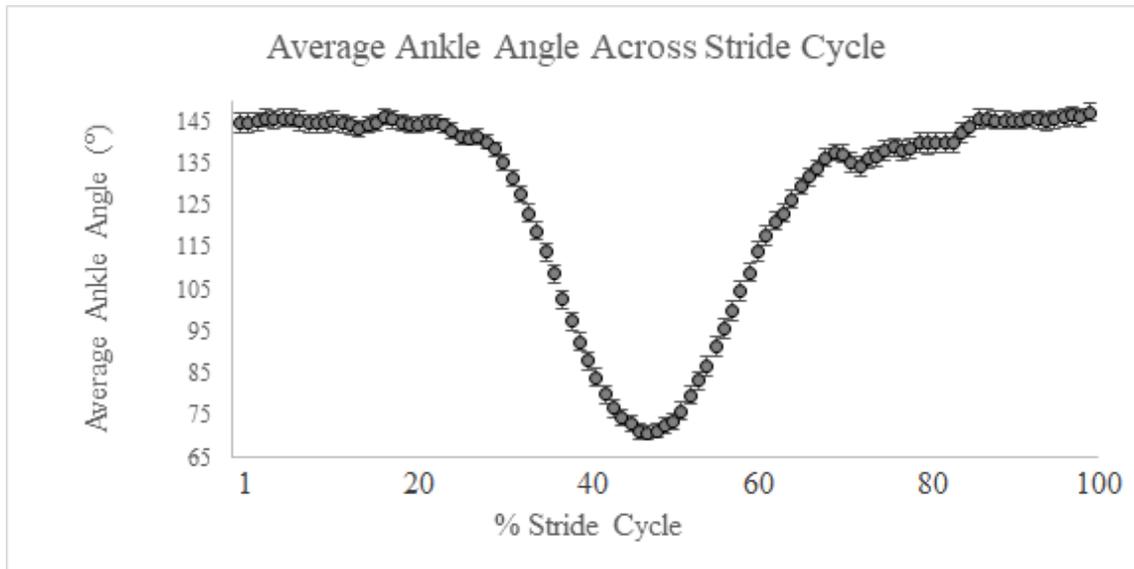


Figure 7: Average kinematic profile of ankle flexion angle throughout the course of a single stride cycle for walking flamingos. All strides across all water depths were normalized to the same duration, with strides in which the ankle was submerged excluded from analysis (pooled $N=5$ animals, 115 strides). Points represent the average value of ankle flexion for each 1% increment of time through the step, with whiskers representing ± 1 standard error.

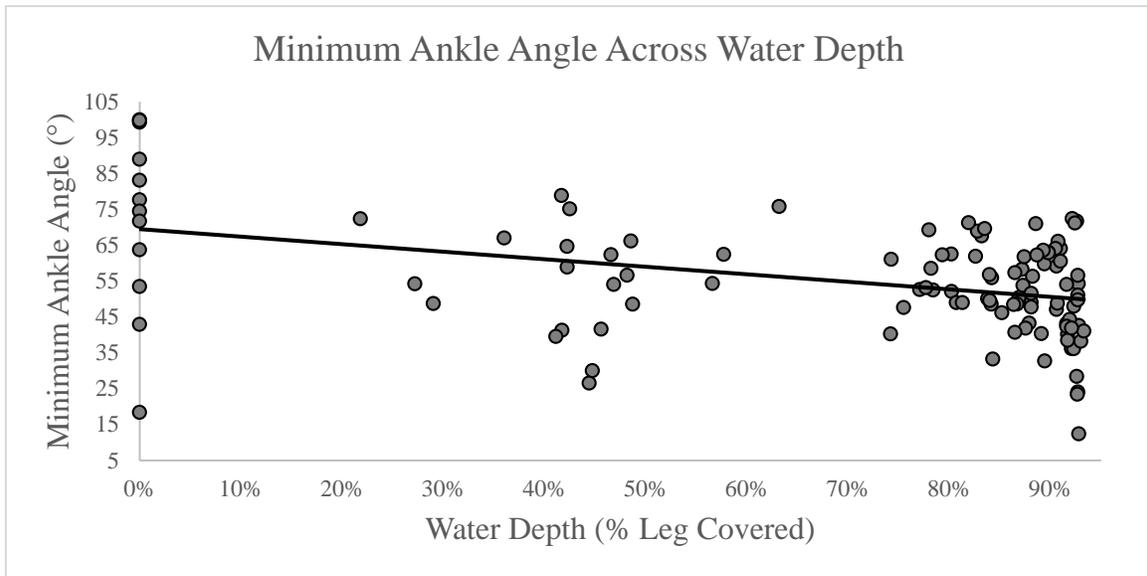


Figure 8: Minimum angle of ankle flexion for flamingos (pooled $N=5$ animals, 115 strides) regressed on water depth. Minimum ankle angles showed a significant trend to be smaller, indicating a more folded leg, in deeper waters.

Tibiotarsus Angle to the Horizontal

The angle of the tibiotarsus with the horizontal was calculated for all strides, such that the minimum angle occurs when the leg is fully off the ground at the highest point of the swing phase, and the maximum angle occurs when the leg is in the middle of stance phase and supporting the weight of the body (*Fig. 9*). Maximum tibiotarsus angles were not significantly affected by water depth (ANOVA, $P=0.4596$, $F=0.55$, $R^2=0.0039$), but this angle is measured when the leg is in stance phase, which is unlikely to yield different values among different environmental conditions. Minimum tibiotarsus angles (*Fig 10*) decreased significantly with increasing water depth (ANOVA, $P<0.0001$, $F=26.27$, $R^2=0.1589$), indicating that the tibiotarsus achieved a more horizontal orientation during wading through deeper water (*Table 1, Figs. 9, 10*).

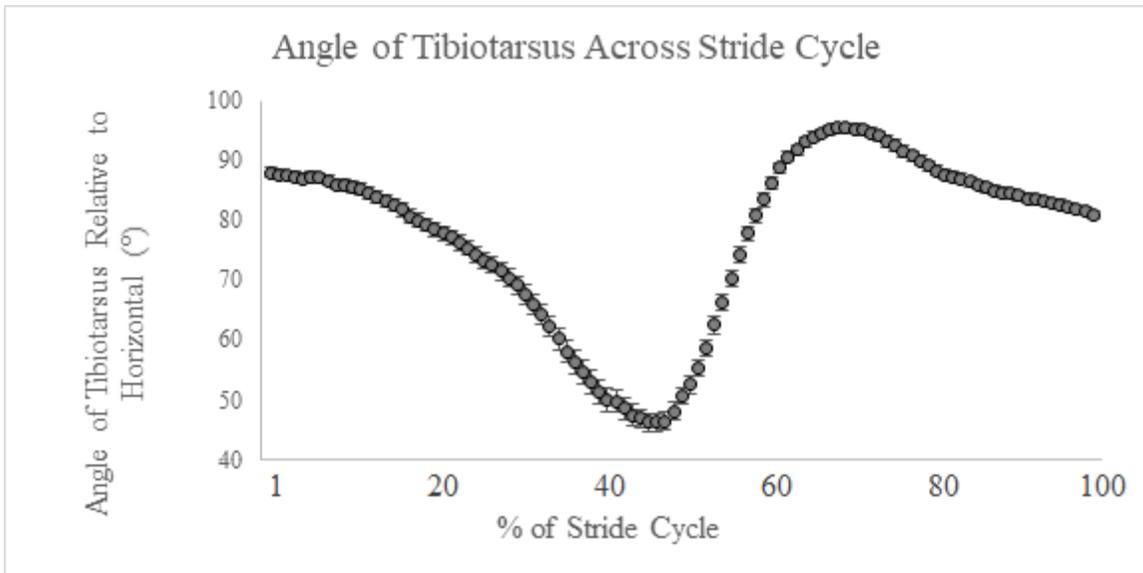


Figure 9: Average kinematic profile of the angle of the tibiotarsus relative to the horizontal throughout the course of a single stride cycle for walking flamingos. All strides across all water depths were normalized to the same duration (pooled $N=5$ animals, 145 strides). Points represent the average value of tibiotarsus angle for each 1% increment of time through the step, with whiskers representing ± 1 standard error.

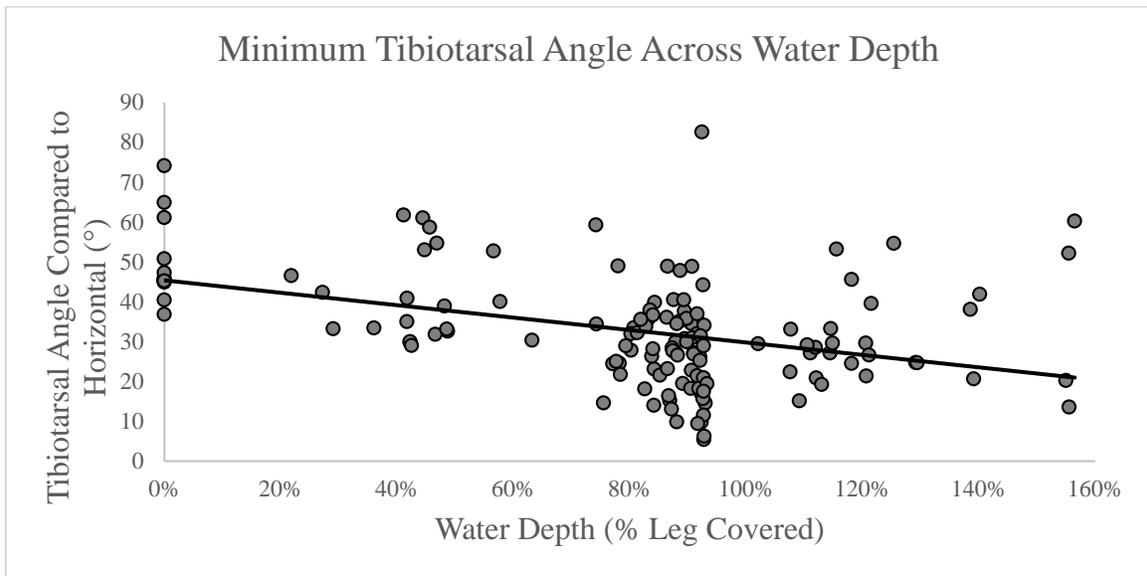


Figure 10: Minimum angle of the tibiotarsal segment compared to the horizontal (pooled $N=5$ animals, 145 strides) regressed on water depth. There was a significant effect of water depth on the minimum tibiotarsal angle, where the minimum angle decreased (became closer to the horizontal) as water depth increased.

Head Angle

The average angle of the head showed little cyclic movement throughout stride cycles across varying conditions of water depth, typically orienting near 90° (Fig. 11). However, the minimum head angle showed a weak, but significant, correlation with water depth (Fig. 12), with larger minimum head angles being used in deeper water (ANOVA; $P= 0.0081$, $F= 7.218$, $R^2= 0.0493$), indicating that the head was held in a slightly more vertical orientation, with the beak tucked closer to the body. In contrast, water depth had no effect on maximum head angle (Fig. 13; ANOVA; $P= 0.9012$, $F= 0.0155$, $R^2=-0.0001$).

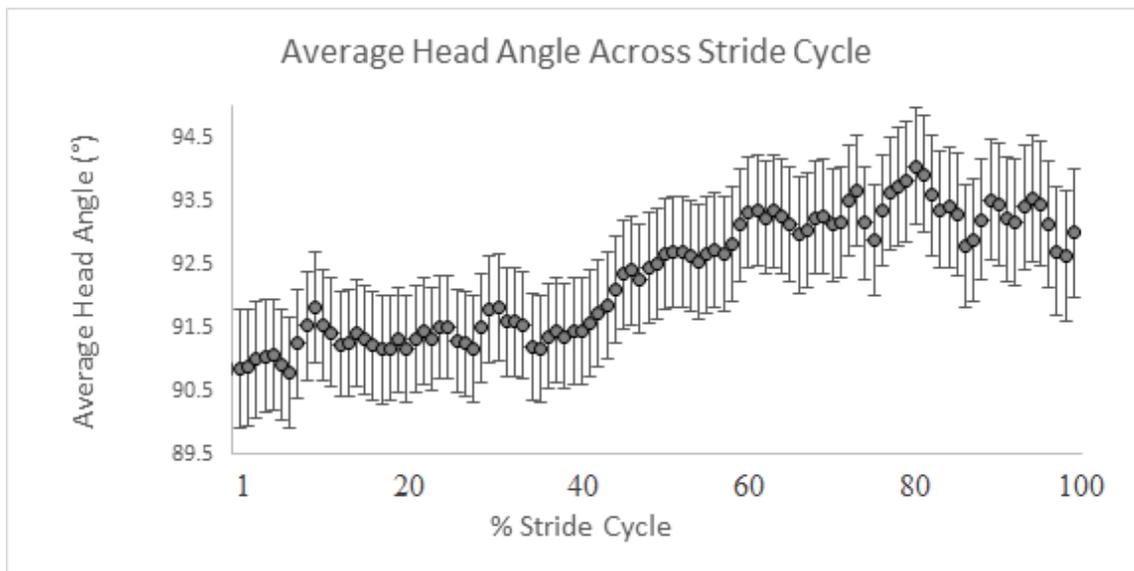


Figure 11: Average kinematic profile of the angle of the head to the horizontal throughout the course of a single stride cycle by walking flamingos. All strides across all water depths were normalized to the same duration (pooled $N=5$ animals, 145 strides). Points represent the average value of head angle for each 1% increment of time through the step, with whiskers representing ± 1 standard error.

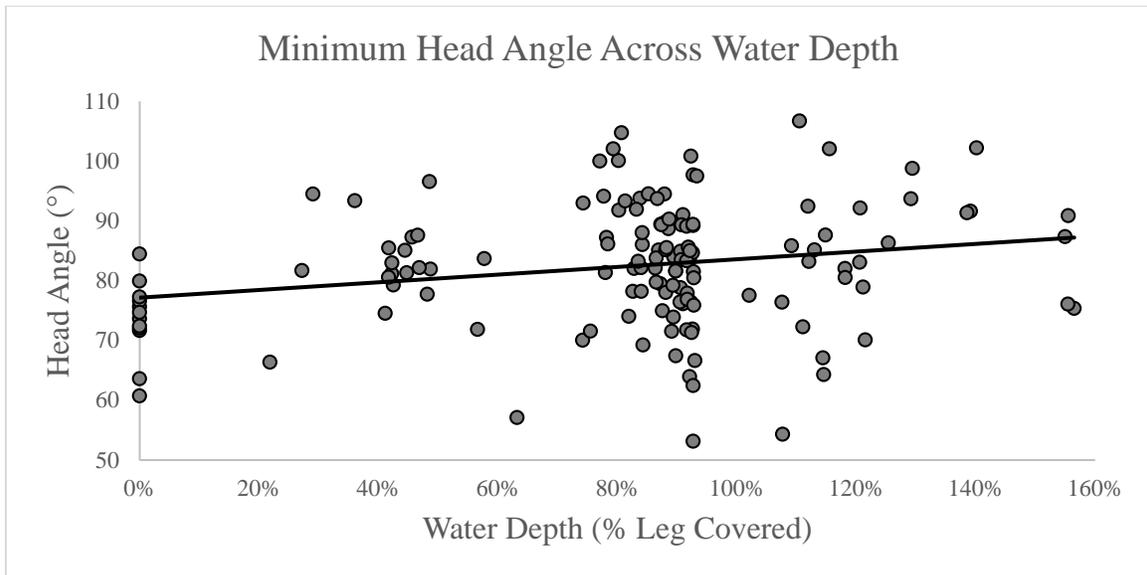


Figure 12: Minimum head angle for flamingos (pooled $N=5$ animals, 145 strides) regressed on water depth. Minimum head angles showed a weak, but significant trend to increase in deeper waters, shifting to a more vertical position.

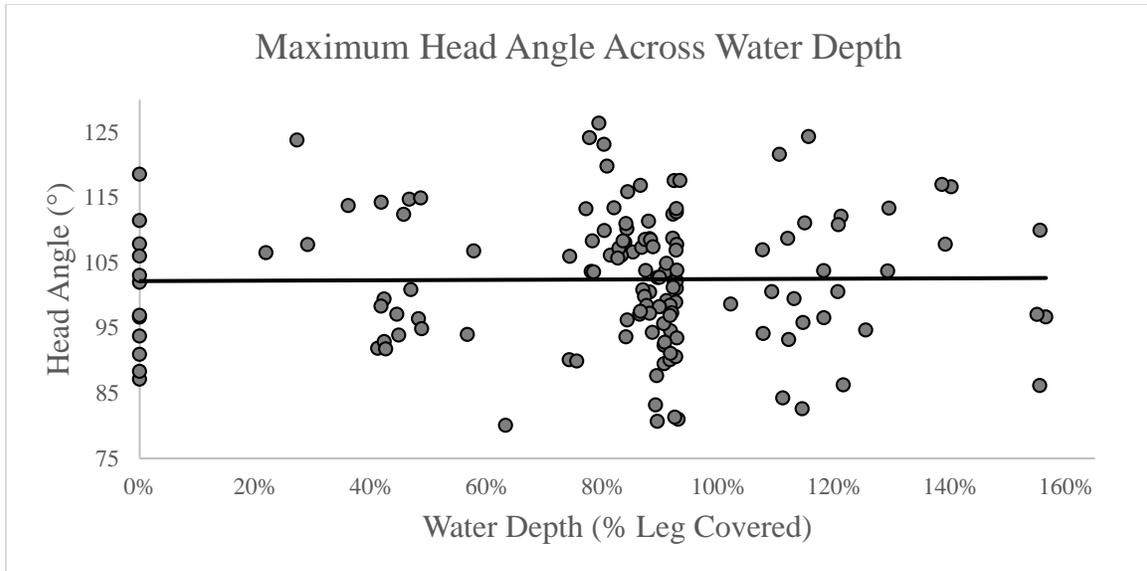


Figure 13: Maximum head angle for flamingos (pooled $N=5$ animals, 145 strides) regressed on water depth. There was not a significant relationship between water depth and maximum head angle.

Distance Between the Head and Body

Similar to head angles, there was little cyclic change in the distance between the head and body of flamingos through the course of steps (*Fig. 14*). There was no significant relationship between water depth and the maximum distance between the body and the head ($P=0.5670$, $F=0.3292$, $R^2=0.0023$; see *Fig. 15*). However, there was a weakly significant relationship between water depth and the minimum distance between the body and head ($P=0.0302$, $F=4.796$, $R^2=0.0333$), with the minimum distance between head and body increasing in deeper water (*Fig. 16*).

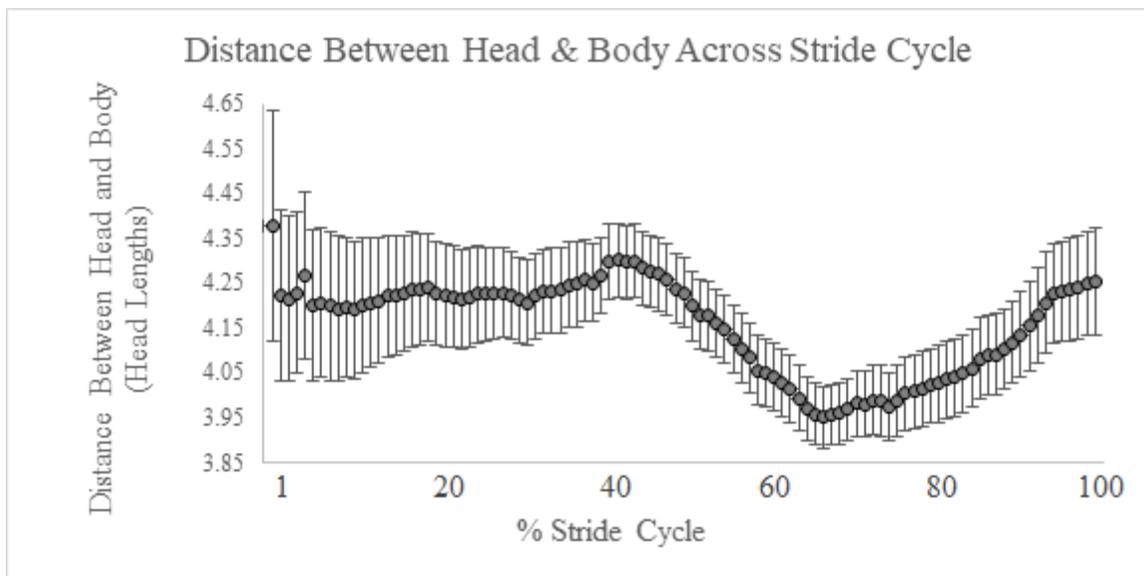


Figure 14: Average kinematic profile of the distance between the head and body (normalized by head length) throughout the course of a single stride cycle by walking flamingos. All strides across all water depths were normalized to the same duration (pooled $N=5$ animals, 145 strides). Points represent the average value of head-body distance for each 1% increment of time through the step, with whiskers representing ± 1 standard error.

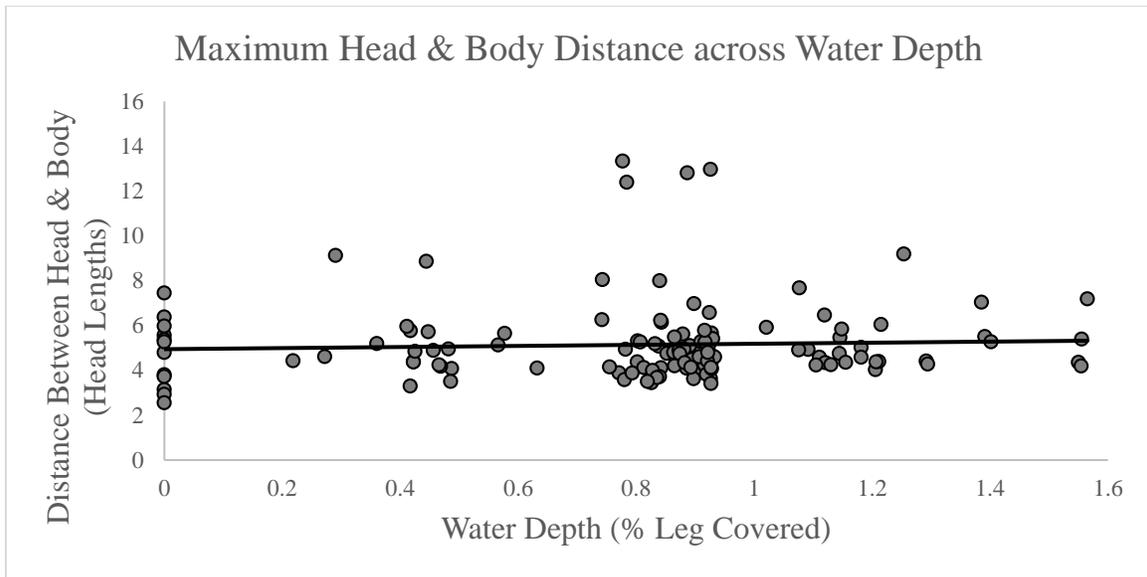


Figure 15: Maximum head-body distance for flamingos (pooled $N=5$ animals, 145 strides) regressed on water depth. There was not a significant relationship between water depth and maximum head-body distance.

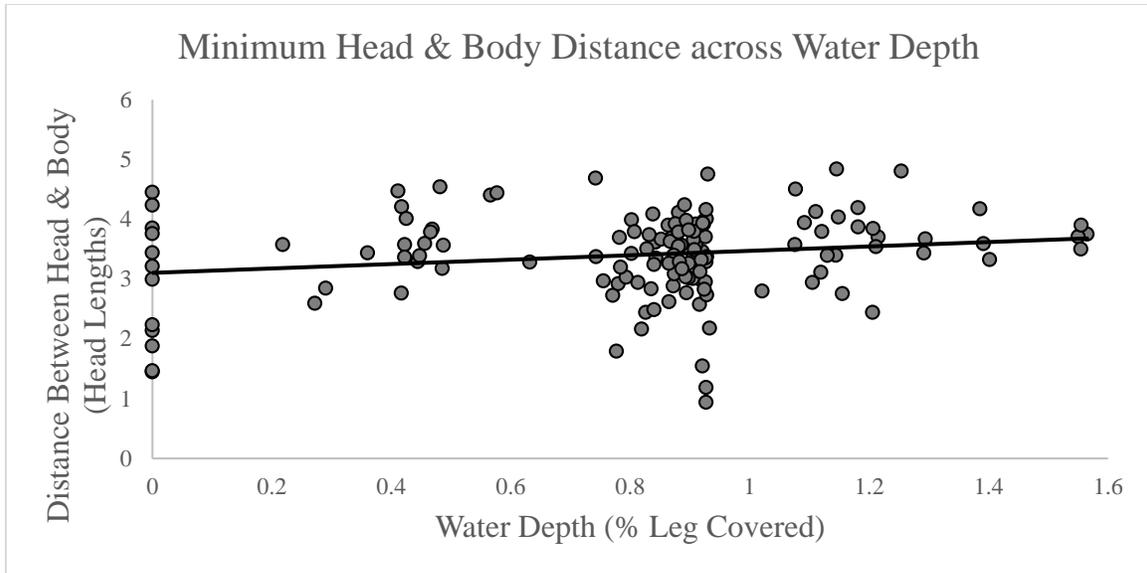


Figure 16: Minimum distance between the head and body for flamingos (pooled $N=5$ animals, 145 strides) regressed on water depth. There was a significant trend for this distance to increase in length in deeper waters.

DISCUSSION

Flamingos exhibit a variety of kinematic changes as they wade through increasing depths of water; however, other kinematic parameters show consistent values despite changes in water depth. These changes can be considered in the context of the locomotor forces most likely to change in correlation with wading depth: drag and buoyancy.

As the limbs of flamingos move through increasing depths of water, they are likely to experience greater drag. There are a variety of strategies that birds could employ to limit such increase in drag. One might be to take higher steps, so that the foot and limb largely step over, rather than drag through, resistive water. Because we could not see through the water in our enclosure, we combined several different measurements to understand how flamingos altered step height in response to water depth. Our primary measurement of step height was the minimum distance between the ankle and the body of the bird. This variable was significantly affected by water depth, where birds took higher steps in deeper water, potentially reducing the drag of the water on the limbs. To further explore the mechanisms by which flamingos achieve greater step heights, we also measured the angle of the tibiotarsus to the horizontal, and the minimum angle of ankle flexion. These measurements showed that the tibiotarsus was raised to significantly more horizontal angles, and the ankle was flexed to smaller angles, as water depth increased. Through such movements, higher steps appear to be achieved through both overall raising of the leg from the knee joint, as well tighter folding of tibiotarsus and tarsometatarsus at the ankle joint. These results suggest that flamingos can exert precisely

controlled motions at multiple joints to lift the limbs and limit drag while wading through deep water.

Despite closing the ankle to a smaller minimum angle in deeper water and the altered movements at the knee to change the angle of the tibiotarsal limb segment, flamingos did not change stride length as they waded through deeper water. It is possible that the exaggeration of step heights could limit the potential for simultaneous kinematic changes that could also increase stride length in deeper water. Such limits to stride length increases might also limiting opportunities for increasing stride velocity in deeper water, as velocity also showed no significantly change across changes in water depth. In the context of these patterns, it is noteworthy that wading behaviors are not significantly more energetically expensive than similar walking behaviors at slower velocities (Halsey et al., 2014). Thus, it is possible that by limiting drag and maintaining consistent velocities, the kinematic changes employed by flamingos might also help to limit increases in their energetic costs as they wade through deeper water.

Beyond changes in limb movements, flamingos also exhibited changes in head position relative to the body in deeper water. In deeper water, the beak was tucked in closer to the body, but the overall distance between the head and the body tended to increase. This could indicate that as water depth increases, flamingos can stretch the neck out further from the body than in shallow water or on land. Reasons why such changes in head position are used are not clear. Nonetheless, such changes in mass distribution might be facilitated by the greater stability conveyed by deep water surrounding the body,

and tucking in the head may improve balance during use of an outstretched neck during deep-water wading.

Species that utilize the interface between land and water must overcome a variety of physical challenges presented by these distinct habitats. Previous studies have suggested that the energetic cost of locomotion in semi-aquatic species may be higher in a given environment than that for an aquatic or terrestrial specialist, though costs for a specialist are typically higher than those for semi-aquatic species in the opposite environmental condition (Fish & Baudinette, 1999). Semi-aquatic species may use a combination of morphological and kinematic adaptations to overcome the increased demands of their unique environmental conditions (Blob et al., 2016). The benefits of access to a broader range of resources, covering both water and land, may provide individuals with sufficient benefits to outweigh the costs associated with locomotion in such challenging environments (Ashley-Ross et al., 2013; Kawano et al., 2013; Blob et al., 2016). While moving between varying water depths, a variety of kinematic changes can be employed to enhance performance, and the changes observed in flamingo locomotion across changes in water depth may reflect such a capacity. Such functional flexibility could be advantageous in shoreline environments where birds must frequently move between land and varying depths of water.

Long-legged birds, which have a distinct limb morphology from other avian species (Zeffer, 2003), have an elevated need for stability. Although large wading birds often possess both long legs and a long neck (Wilkinson & Ruxton, 2011), with flamingo taxa having the longest legs and neck relative to the body (del Hoyo, 1994), smaller

wading species (e.g. yellowlegs, sandpipers) typically have elongated legs without extreme elongation of the neck (Baker, 1979). Future studies that compare wading kinematics between large and small species of waders could provide insight into the role of neck and head movements in wading function. Such work might also provide a model for the design of bioinspired vehicles capable of stable and energy efficient locomotion through a variety of habitats (Hugel et al., 2003). Comparative data across wading species could also inform the design of zoological enclosures, helping to ensure that captive wading birds are kept in areas that limit locomotor difficulties. Such applications provide motivation for further study of the abilities of diverse taxa to move through complex physical environments.

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