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# Conquering Visual Challenges While Hunting Across the Air-Water Interface; a Study of Foraging Day Herons

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Conquering Visual Challenges While Hunting Across the Air-Water Interface;

a Study of Foraging Day Herons

Holly Kay Milton Brown, PhD

University of Connecticut, 2017

If spearfishing were easy, few would use hook and line. Among several visual challenges of hunting across the air-water interface are sun glint, which causes glare, making it hard to see below the water surface; and refraction, which causes submerged prey items to appear where they are not. These challenges are exacerbated by the fact that prey have visual (and other sensory) adaptations that allow them to detect/recognize potential predators. In order to forage successfully on underwater prey, cross-media hunters must be able to compensate for these visual challenges, yet we know very little about their compensatory mechanisms. *Ardea* and *Egretta spp.* (herons) are ideal model systems for studying how predators compensate for visual challenges at the air-water interface; they are visually-hunting, piscivorous birds. They also regularly perform a behavior called “head-tilting,” which I hypothesized could be involved in compensating for all three of the aforementioned challenges: glint, refraction, and being detected by prey. Further, I hypothesized that herons would orient away from the sun in order to mitigate the amount of sun glint in their fields of view, while actively foraging. In this body of work, I have used field observations to estimate body orientations of free-living foraging herons. I used high speed videography of free-living, foraging herons, three-dimensional digitization techniques, three-dimensional trigonometry, and optical modeling of sea surface reflectance to test whether head-tilting was related to sun glint or refraction.

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Lastly, I exposed predator-naïve brown trout to heron decoys in upright versus head-tilted positions, and used two-dimensional digitization of flight distances to test whether prey were less likely to recognize the head-tilting decoy as a predator than the upright heron. My work suggests that herons are not behaviorally mitigating glint via body orientation or via head-tilting. Further, they are not using head-tilting to aid in refraction correction. However, I found some evidence that herons use head-tilting to evade being detected or recognized. This hypothesis should be examined further.

Conquering Visual Challenges While Hunting Across the Air-Water Interface;  
a Study of Foraging Day Herons

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A Dissertation

Submitted in Partial Fulfillment of the

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Doctor of Philosophy

at the

University of Connecticut

2017

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2017

APPROVAL PAGE

Doctor of Philosophy Dissertation

Conquering Visual Challenges While Hunting Across the Air-Water Interface;  
a Study of Foraging Day Herons

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2017

## Dedication

To all of the educators who refuse to give up on young people, especially Dominic Cammarota, and the late Eleanor Archie: thank you for caring so much. I might not have made it past the 9<sup>th</sup> grade without you.

To my whole family – biological relatives, step-family and in-laws: thank you for your love and support. My mother, Janis Brown, and my husband/best friend, Arnell Milton Brown have been especially patient amidst all of my endeavors. And my father, Oliver Brown, encouraged me when I was having second thoughts about coming back to school.

To all of my friends, and especially to Sarah Eisele-Dyrli, Ambika Kamath, Cera Fisher, Adriana De León, Winnie Wong, and my SCC family: one could spend a life time looking for friends as fantastic as you. Thank you for the many ways in which you've supported me.

To my advisor, Margaret Rubega: being mentored by you has been the *privilege* of a lifetime.

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Additionally, I want to thank my collaborators: Margaret Rubega (all chapters), Heidi Dierssen (chapter 1), C. Seabird McKeon (chapter 2), and Anthony Rizzie (chapters 2 and 3). Furthermore, several other people offered critical feedback on these works, including Eric Schultz (committee member), Eldridge Adams (committee member), and Andrew Moiseff (committee member). I would also like to thank everyone in the University of Connecticut Ornithology Group past and present, especially, Chris Elphick, Morgan Tingley, Alejandro Rico-Guevara, Diego Sustaita, Kevin Burgio, Alyssa Borowske, Christopher Field, Manette Sandor, and Jacob Socolar for helpful edits and advice. I am also grateful to Ambika Kamath for reviewing several iterations of research proposals.



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## **Dissertation Introduction**

Hunting across the air-water interface, also called cross-media hunting, has independently evolved multiple times in fish, reptiles, birds, mammals, and even spiders. I am particularly interested in cross-media hunters that use vision as their dominant sense for hunting, that hunt from air to water (and not from water to air), and that hunt diurnally, because these animals encounter several visual challenges at the air-water interface. For example, if you Google a picture of a sunset over water, you will find that it is almost always impossible to find any fish (or other aquatic prey) in the water, largely due to the blinding effect of the direct reflection of sunlight off of the water surface. This direct reflected light is called glint, and it obscures the view of any objects (e.g., prey) beneath the surface. Even if an animal manages to orient in such a manner that glint is reduced, it still must face the problem of refraction, or the bending of light as it passes through media of different densities, which causes prey to appear in locations where they are not. However, even if the animal is able to compensate for glint, and correct for refraction, it still must encounter the problem of possibly being detected by prey, otherwise their prey might flee before they have the chance to strike. So the air-water interface is a seemingly tough place to make a living. Yet, about 50 million years ago, birds became some of the most successful invaders of this cross-media hunting niche. The goal of my dissertation work has been to uncover some of their secrets by testing hypotheses about ways in which they might have solved these vision-related problems.

## **CHAPTER ONE**

**Using quantitative optical models to understand heron foraging behavior in relation  
to light reflected from the air-water interface**

Collaborators: Margaret Rubega and Heidi Dierssen

## 1.1 Abstract

Multiple lineages of birds have independently evolved foraging strategies that involve catching aquatic prey by striking at them through the water's surface. Diurnal, visual predators that hunt across the air-water interface encounter several visual challenges, including sun glint, or reflection of sunlight by the water surface. Because intense sun glint is ubiquitous at the air-water interface, and obscures visual signals from submerged prey, visually-hunting, cross-media predators must solve the problem of glint to hunt effectively. One obvious solution is to turn away from the sun, but turning too far will cast shadows over prey, causing them to flee. Our ability to understand how predators achieve a solution to glint is limited by our ability to quantify the amount of glint that free-living predators are actually exposed to under different light conditions. Herons (*Ardea spp.*) are a good model system for answering questions about cross-media hunting because they are conspicuous, widely distributed, and forage throughout a variety of aquatic habitats, on a variety of submerged prey. We examined whether foraging herons orient away from the sun in order to avoid glint effects. We employed radiative transfer modeling of water surface reflectance, drawn from optical oceanography, in a novel context to estimate the visual exposure to glint of free-living, actively foraging herons. We found evidence that *Ardea spp.* do not use body orientation to compensate for sun glint while foraging. Instead, they tended to adjust their position to face into the wind at higher wind speeds. Since herons are not using body orientation to reduce their exposure to glint, they must have some other, not yet understood, means of compensation, either anatomical or behavioral. We suggest that radiative transfer

modeling is a promising tool for elucidating the ecology and evolution of air-to-water foraging systems in birds.

## **1.2 Introduction**

Birds have repeatedly, and independently, evolved foraging strategies that involve detecting prey in water, and striking at them through the air-water interface. To do so successfully, they must contend with a number of visual challenges imposed by the optical properties of the water itself. First, water surfaces can reflect light. Sun glint (also called “glitter”, or inaccurately called “glare”; hereafter, “glint”) refers to the reflection of sunlight by a water surface, directly toward the viewer. Glint obscures detection of upwelling light from beneath the surface of the water, making it more difficult to see objects below the surface.

Since cross-media predators, by definition, are attempting to locate submerged prey, we expect them to have evolved ways to compensate for the effect of glint. One obvious method of reducing the effect of glint is to turn away: an animal that forages at the air-water interface should orient itself generally away from the sun under clear sky conditions if it aims to reduce visual exposure to glint. But by how much? The amount of glint exposure is a complex function of the viewing direction, field of view of the detector or eye, topography of a wind-blown sea surface, sun elevation and the spectral distribution of light.

Radiative transfer modeling, used in optical oceanography, has shown that glint is generally reduced with an increasing difference in bearing from the sun (Mobley 1999). For example, assuming 5 m/s wind, a sun elevation of  $60^\circ$ , and a viewing angle looking  $40^\circ$  downward with respect to the horizon, the sea surface would reflect only about 3% of the skylight incident upon the sea surface for an animal viewing the sea surface facing directly opposite ( $180^\circ$ ) to the sun's bearing. This percentage remains fairly similar until the viewer is facing perpendicular ( $90^\circ$ ) to the sun's bearing, but begins to rise fairly quickly thereafter, to about 12% when facing directly into the sun's bearing (Fig. 7 in Mobley 1999).

However, aquatic birds that hunt during the daytime must compensate for an additional, and opposing, challenge: they must be within striking distance of their prey without causing prey to flee. While glint is lowest at  $180^\circ$  to the sun's bearing, this is also the bearing that would cause a predator to hunt directly into its own shadow. Several aquatic prey species are known to flee when shadows pass overhead (e.g., Forward 1977; Roberts 1978, Yoshizawa and Jeffery 2008). Therefore, a bird hunting across the air-water interface on a sunny day is likely trading off its ability to see prey against the prey's ability to see them.

Mobley (1999) used radiative transfer modeling to show that when orienting a light detector at about  $135^\circ$  away from the bearing of the sun while measuring remote sensing



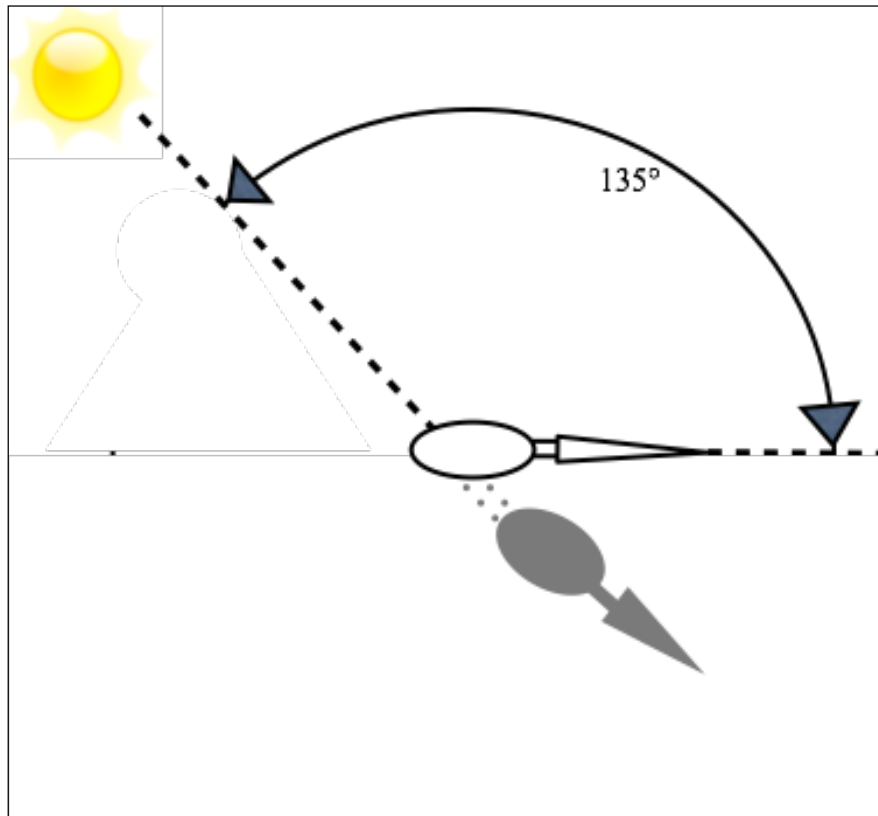
reflectance of oceanic environments, the view of glint from the water surface is as low as possible over a wide range of water surface and environmental conditions, without facing directly into self-shadow.

Mobley's work, by extension, suggests that while there is a range of orientations at which birds could reduce their exposure to glint, orienting at  $135^\circ$  to the bearing of the sun is the position in which birds hunting across the air-water interface can best trade off reducing glint exposure, while also avoiding casting shadows over potential prey.

This logic assumes that birds see and perceive glint as we do, an assumption that may not be justified, given the limitations on what we know about avian vision. Nonetheless, there is some limited, and anecdotal evidence that they do and that they may be trading off glint exposure against their own detectability as we predicted based on Mobley's (1999) radiative transfer modeling. For example, Brown Pelicans (*Pelecanus occidentalis*), were found to orient at an average of  $135.6^\circ$  to sun bearing (s.d. =  $36.1^\circ$ ) as they dove for fish (Carl 1987). We have also documented that a tern diving for fish in a pond, did so at about  $140^\circ$  to sun bearing, (documented on video three times in a row; it also did so several times in a row before the lead author started recording the behavior; Supplemental Video 1). Even the behavior of non-aquatic avian predators suggests that they experience challenges from intense light conditions as we do. When the dark facial masks on Masked Shrikes (*Lanius nubicus*) were painted white, they oriented away from

the sun to a greater degree than shrikes with black masks (Yosef et al. 2012), suggesting that sunlight reflecting from their facial feathers caused some visual discomfort.

Visual ecologists have demonstrated that orientation is important in visual function (e.g., Muheim et al. 2006, Penacchio et al. 2015), but there are only a handful of studies that investigate orientation specifically with regard to hunting strategies (Carl 1987, King and LeBlanc 1995, Yosef et al. 2012, Huveneers et al. 2015). Orientation with respect to the sun may affect the ability to see prey, and therefore should be explicitly considered when studying the foraging ecology of visual, cross-media predators. Here, we examine the hypothesis that avian cross-media predators use body orientation to reduce glint in their strike zones while hunting, and that they do so in a manner that trades off glint exposure against self-shadow into their strike zones (Fig. 1). In order to test this hypothesis, we studied diurnal herons of the genus *Ardea*, which belong to a clade of piscivorous birds that have been specializing to hunt across the highly reflective air-water interface for over 50 million years.



**Fig. 1.** Overhead view of a foraging heron. We predicted that herons would orient generally away from the sun to minimize visual exposure to glint; if they also avoid casting shadows over prey (which alert prey to their presence), we predict that they will orient at about 135° away from the bearing of the sun. (Figure produced in MS Excel.)

We studied, specifically, two daytime-active herons, Great Blue Herons (*Ardea herodias*) and Great Egrets (*Ardea alba*; hereafter, “herons”). These species are good models for answering questions about cross-media hunting because they are numerous, conspicuous, widely distributed, and forage throughout a variety of aquatic habitats, on a variety of submerged prey. If herons were using orientation to trade off glint and self-shadow, we predicted that they would: a. orient in ways that minimize glint, and maximize the signal from upwelling light (i.e., the light reflected by potential submerged prey items), as compared with what would be expected if heron orientation were random, and b.

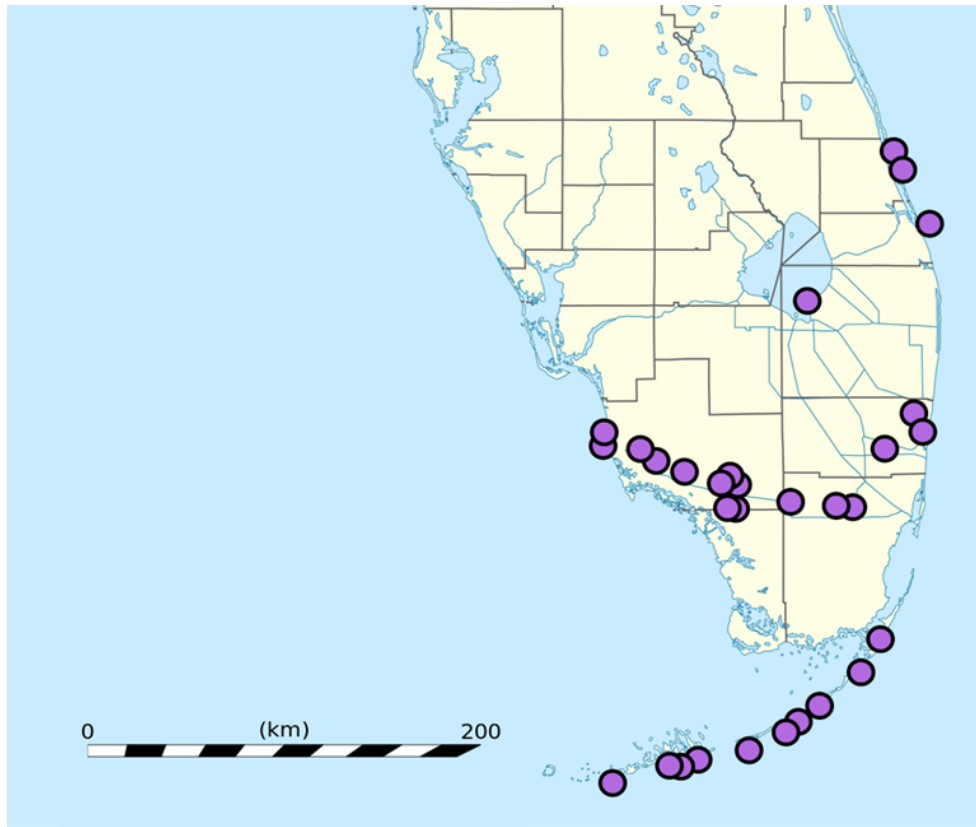
specifically, we expect them to orient at an average of  $135^{\circ}$  to the sun bearing. Great Blue Herons tend to be slightly more crepuscular than the more diurnal Great Egrets (e.g., McNeil et al. 1993; HMB personal observation). In gathering data from both, our intent was to obtain generalizable information about how herons might compensate for glare while hunting through the air-water interface, over a wide range of daylight conditions. We employed radiative transfer modeling in a novel context to directly estimate the actual exposure of individual birds to glint, on the basis of their orientation to the sun, the sun elevation, and light conditions.

We also considered the hypothesis that heron body orientation could be related to wind. Orientation with respect to both sun position and wind direction have been widely recognized as important physiological mechanisms by which animals regulate body and microhabitat temperatures (e.g., Orr 1970, Walsberg 1993, Fortin et al. 2000, and many others). If herons were orienting to prevent loss of body heat, we predicted that heron orientation would correlate with wind direction, particularly at higher wind speeds. While the two hypotheses are not necessarily opposed under all conditions, we predicted that they would be more likely to face into the wind, regardless of sun position, as wind speed increased.

### **1.3 Materials and methods**

In June 2013, January 2014, and January-February 2015, we opportunistically obtained 279 observations of 68 free-living, foraging herons in southern Florida (Fig. 2). As our study involved focal animals in the field, it was not possible to record data blind. In areas where an individual heron seemed to be actively guarding a foraging area (e.g., by chasing other individuals away), we sampled the site only once. However, in areas where there were several herons foraging, we were able to obtain observations of different individuals at the same location. From a minimum distance of 20m, using binoculars (Nikon Monarch 3, 10x42), we observed individual foraging herons, and recorded up to 6 instantaneous samples of their body and head orientations, or fewer, if the individual flew away. In 2013, instantaneous samples were spaced 5 minutes apart, while in 2014 and 2015 samples were taken every two minutes. At the beginning of each observation, we noted the date, time, and the species. We noted sun visibility and cloud cover, as our predictions depended on the sun's being visible. We also noted wind bearing and speed category (calm/virtually undetectable; leaves rustle; branches sway; trees sway). If the wind speed and direction were noticeably variable, we updated this information during every instantaneous sample. We also noted whether or not the bird's shadow was obstructed (e.g., by emergent vegetation) during every instantaneous sample. The orientation of the birds' bodies and heads, and the orientation of the wind were estimated in the field with a handheld compass. Exact sun bearing and elevation were later retrieved from the National Oceanographic and Atmospheric Administration's online sun position calculator, based on the time recorded for each instantaneous sample in each observation.

Also, the approximate latitude and longitude of each location were obtained from Google Earth. We were then able to calculate the estimated orientation differences between the birds and the sun, and between the birds and the wind, to use in analyses. After the final field season, we quantified error associated with estimating heron orientation. To do so, a field assistant placed a Great Blue Heron lawn ornament in 24 different directions and recorded its real orientation while the lead author (who made all compass measurements in the field) estimated each orientation from a distance of 20m, with the same binoculars that were used in the field (Nikon Monarch 3, 10x42). Our estimations of body orientations of a Great Blue Heron lawn ornament were within an average of  $9.3^{\circ}$  (s.d. =  $7.5^{\circ}$ ,  $N = 24$ ). Therefore, we believe our estimates of heron body orientation are sufficiently accurate to test the hypotheses of interest in this study.



**Fig. 2.** Map of southern Florida, USA. Circles indicate where data were collected. Some circles overlap more than one sampling location. This map was modified from the original, which was created by Eric Gaba, via Wikimedia Commons (user ID: Sting).

Using the *Hydrolight*® radiative transfer model (Mobley 1998), we estimated absolute and relative glint in the green spectrum (550 nm). We defined relative green glint as green glint divided by the all incoming green light in the field of view (i.e., water-leaving radiance plus radiance reflected by the sea surface). The relative measure is a type of signal-to-noise measurement. We used green light exclusively, because we wanted our estimates of glint to be conservative, in that they would maximize background brightness and minimize relative glint. In general, green light penetrates furthest into coastal waters

(Kirk 2011), and is therefore the light most available to be reflected by the seafloor, and exit the water as upwelling light. Therefore, in comparison, the contribution of glint is lower relative to the upwelling light in the green spectrum versus in other spectral regions.

We also used conservative but realistic values representing conditions in Florida, and conditions for wild foraging herons, for all variables in *Hydrolight*®, in order to obtain conservative estimates for glint. We modeled reflectance for a light-colored sand (ooid), which is both typical of many Florida coasts, but also creates high reflectance off of the sea floor, thus increasing the relative signal of upwelling light as compared with glint. We used a medium value for light attenuation in the water by indicating that light would attenuate by half for every meter below the sea surface (McPherson et al. 2011). We also used a water depth of 28 cm based on multiple records of the water depths in which herons forage in Florida (Powell 1987, Bancroft et al. 2002). We ran the model under two wind conditions: 5 m/s, and 10 m/s. We also ran each of those models under two light conditions: where the sun was visible, and where it was obstructed by clouds.

To continue in our effort to gain conservative absolute and relative estimates of green glint, we also only retrieved outputs from a viewing direction of 40° to the nadir, because this viewing direction minimizes the proportion of skylight reflected at the sea surface under multiple wind speed scenarios (see Fig. 6 in Mobley 1999).



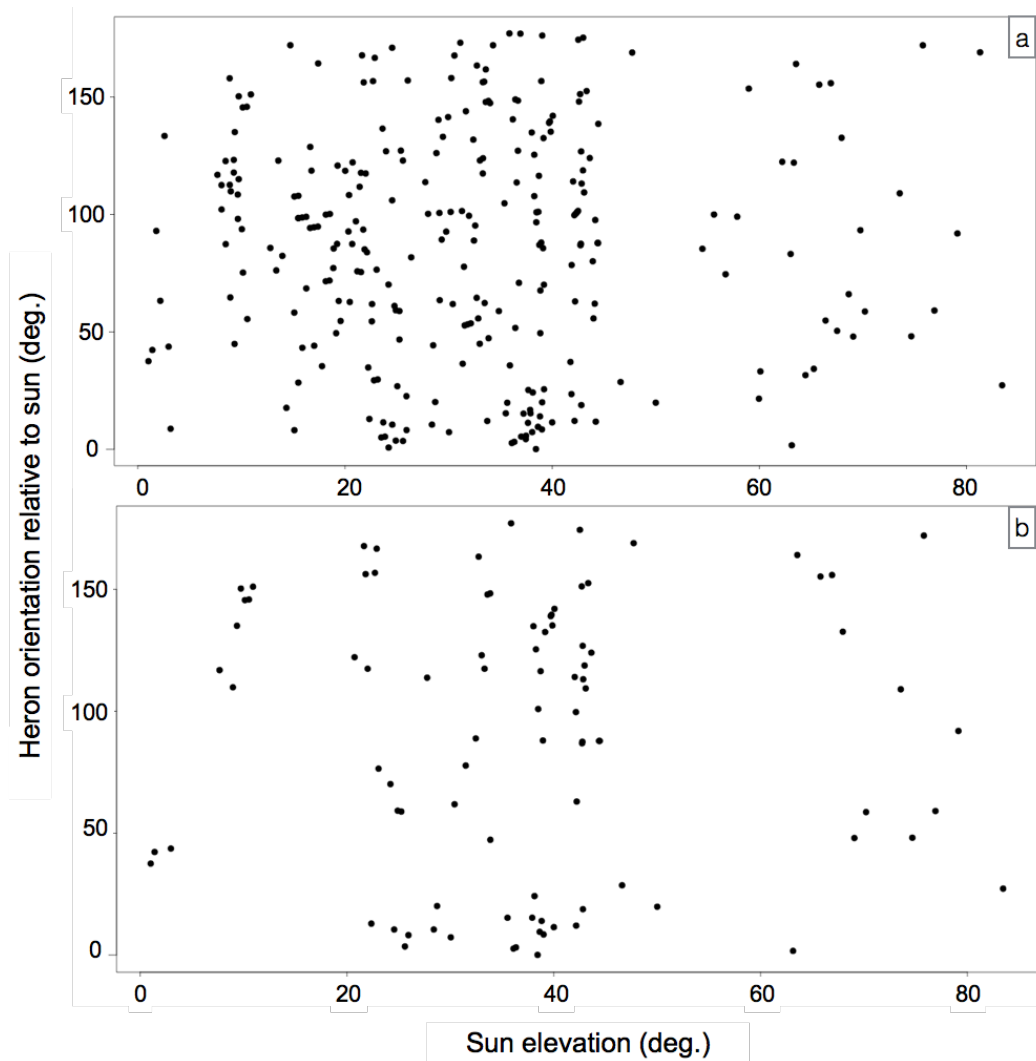
We generated interpolated heat maps of absolute and relative glint in MATLAB (2015), using estimates based on sun elevations of 0, 15, 30, 45, 60, 75 and 90° from the horizon. Finally, we used two-sample t-tests to compare estimates of visual exposure to glint for each heron body orientation with estimates of glint exposure that we would expect if heron orientation were random, using coordinates generated from random.org, to test the prediction that herons would orient in a manner that reduced visual exposure to glint.

All other statistical analyses were performed in R (R Core Team 2013). To examine heron orientation relative to sun position, we used only instantaneous samples where herons' heads were oriented in the same direction as their bodies, and where the herons' shadows were cast over water (i.e., unobstructed by emergent vegetation, and not cast onto land), and the sun was at least partially visible. To test the prediction that herons would orient 135° to the bearing of the sun, we regressed the absolute difference between sun bearing and heron bearing (i.e. heron orientation relative to sun bearing), against sun elevation, using generalized estimating equations (Liang and Zeger 1986) with the “geepack” package in R (Højsgaard et al. 2006). We used sun elevation as the independent variable instead of time, in order that we were comparing heron orientations under consistent sun positions each day. We used generalized estimating equations to account for use of multiple observations for some individuals, which are likely correlated. Thus, we used “individuals” as grouping factors in our model. We also used unstructured correlation matrices because we were unsure of what, if any, kind of relationship there might be among intra-individual data points. We then used the Wald-statistic to test the

overall significance of the regression. As there is no package to estimate power or effect size based on a Wald test, at present, we estimated the effect size of our findings using a power analysis based on a generalized least squares linear model of our data using the “pwr” package (Champely 2015). We similarly regressed the absolute value of the difference between the orientations of the wind and the heron versus wind speed category, and conducted a power analysis.

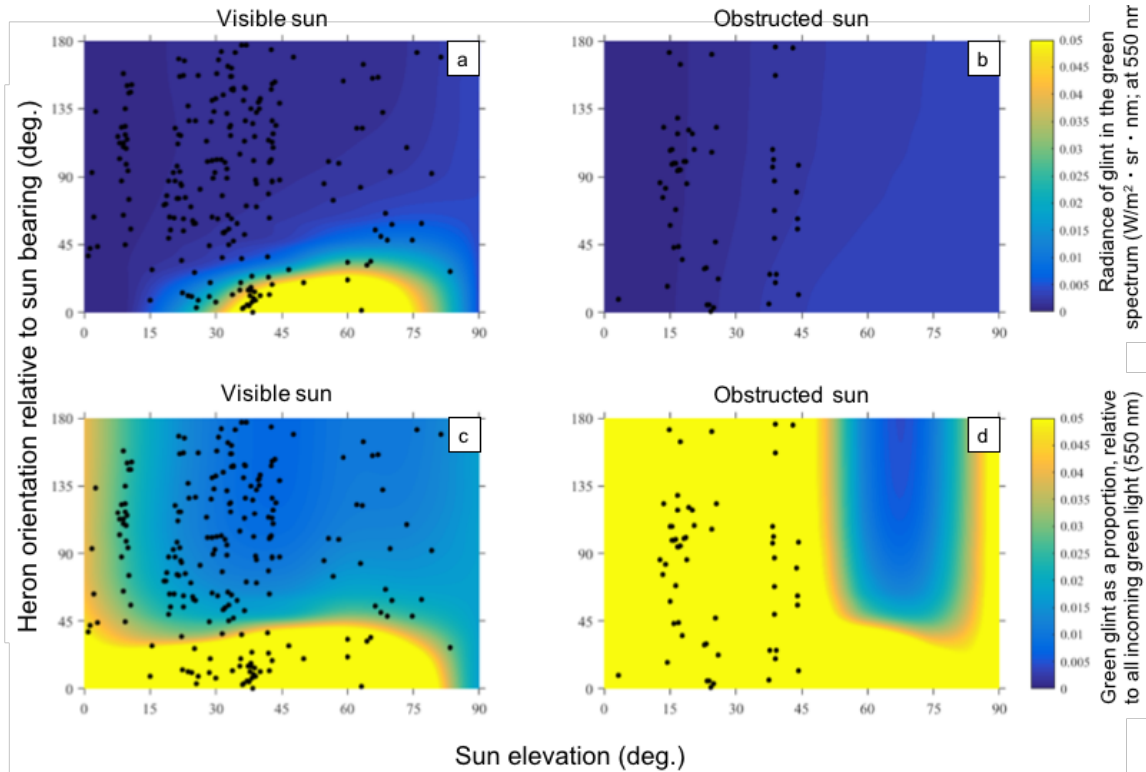
#### **1.4 Results**

Our prediction that herons would orient in a manner that suggested trading off reducing glint and self-shadow in their strike zones was not supported. We detected no departures from random orientation with respect to sun bearing in herons, across all sun elevations ( $y = 89.37 - 0.02x$ ;  $W = 0.003$ ;  $p = 0.96$ ). This held true no matter whether we included the whole data set in the analysis, or just the subset of the data from when both the sun and the heron’s shadows were visible (Fig. 3a-b). The calculated effect size when regressing heron orientation relative to sun bearing versus sun elevation was miniscule ( $[r^2 / (1 - r^2)] = \sim 0.0002$ ).



**Fig 3a-b.** Scatterplots of our data, using points where heron's head and body orientations were in parallel. In both graphs,  $0^\circ$  on the x-axis indicates that the sun is on the horizon, and  $90^\circ$  indicates that the sun is overhead. On the y-axis,  $0^\circ$  indicates that the heron was facing directly into the sun, and  $180^\circ$  indicates that the heron was facing opposite to the sun. **a.** Using the whole data set, note that heron orientation with respect to sun position does not support our predictions, but rather appears random ( $p = 0.95$ ). **b.** Using only data points where the sun was unobstructed (e.g., by clouds) and the heron's shadow was unobstructed (e.g., by emergent vegetation) thins the data substantially, but does not change the overall lack of pattern ( $p = 0.96$ ). (Figures produced in R and edited in Keynote.)

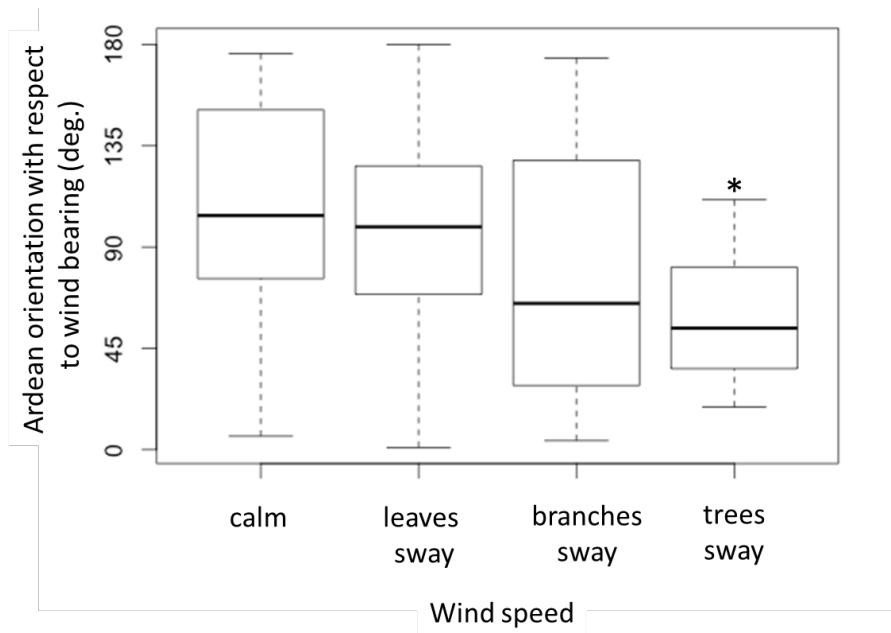
Overlaying our orientation data onto our heat maps displaying absolute and relative estimates of green glint added further evidence that herons are not using body orientation to reduce visual exposure to glint (Fig. 4). We decided to use only the heat maps we generated for 5 m/s wind speed for analyses because the heat maps generated for 10 m/s wind appeared nearly identical. There was no difference between the glint estimated at each heron orientation to the sun and glint that would be experienced at random, either in absolute ( $t = 1.76$ ,  $p = 0.08$ ) or relative estimates of green glint ( $t = 1.55$ ,  $p = 0.12$ ) with a visible sun. With a completely obstructed sun, glint was still no different from random for absolute ( $t = 0.14$ ,  $p = 0.89$ ), or relative estimates of green glint ( $t = 1.10$ ,  $p = 0.27$ ).



**Fig. 4.** Heat maps that indicate measures of green sun glint (550 nm) directed at the viewer when wind is 5 m/s, by absolute (**a**, **b**) and relative (**c**, **d**) measures. (Heat maps for wind speeds of 10 m/s were nearly identical, and are not shown here.) Our orientation data from Fig. 3b are superimposed on these heat maps by sun visibility: sun visible (left)

and sun obstructed (right). Note that herons are orienting randomly, *and* they are foraging in “hot spots” where glint is maximized. (Figure produced in MATLAB and edited in MS Excel.)

In support of our last hypothesis, herons tended to face head-on into the wind at the highest wind speeds in our study, which were over about 10 m/s ( $W = 0.57$ ,  $p = 0.44$  in calm wind conditions;  $W = 3.48$ ,  $p = 0.06$  at moderate wind speeds;  $W = 9.74$ ,  $p = 0.002$  at the highest wind speeds; Fig. 5). This result had very high power (power estimated using generalized least squares model as a proxy = 0.96).



**Fig. 5.** Box plot of heron orientation with respect to the bearing of the wind by wind speed category. On the y-axis,  $0^\circ$  indicates that the heron was facing directly into the wind, and  $180^\circ$  indicates that it was facing opposite to the wind. Herons faced more directly into the wind when branches began to sway, or at wind speeds of about 5 m/s ( $p = 0.06$ ) and when trees began to sway, or at wind speeds above 10 m/s ( $p = 0.002$ ). (Figure produced in R and edited in Keynote.)

## 1.5 Discussion

Our data provide strong evidence that herons are not using body orientation with respect to sun position as a behavioral mechanism for reducing glint in their strike zone. Herons, when foraging through the highly reflective air-water interface, are not avoiding orienting in directions with the highest estimated exposure to glint, whether in absolute terms, or relative to incoming light, and they are not trading off glint and shadow in their strike zones.

Our data also showed that as wind speed increased, herons tended to face more head-on into the wind. In retrospect, this is not surprising. One likely explanation for orienting to the wind is that herons are orienting for thermoregulatory purposes. Facing into the wind has been shown to decrease heat loss in birds (e.g., Fortin et al. 2000).

Herons, and other cross-media hunters, may compensate for glint in other ways. Krebs & Partridge (1973) hypothesized that Great Blue Herons tilt their heads and long necks toward the sun – in a foraging behavior known as “head-tilting” – to effectively shift a perceived area of glare out of their intended strike path. However, their idea was not fully tested, and further research is required to assess whether herons are head-tilting to compensate for glint effects, or has a different function.

Because light that is reflected from water surfaces is polarized, some form of polarization vision could be useful to cross-media hunters. We are unaware of any evidence for anatomical features that act as filters to exclude polarized light (as polarized sunglasses would) in any natural visual systems. However, there is considerable evidence that animals across many taxa can see patterns of light polarization, including some behavioral evidence in birds (reviewed in Muheim 2011). This type of polarization sensitivity could potentially be helpful to cross-media predators, as it might allow them to detect and compensate for the horizontally polarized light present in glint. We suggest that behavioral studies designed to detect whether avian cross-media predators exhibit polarized light sensitivity would be fruitful for understanding the ability of these birds to hunt successfully in the face of intense glint.

Hérons may be a good system in which to look for a mechanism for polarization vision in birds, since they do not seem to be behaviorally compensating for glint. To date, we only have some very basic details about herons' visual anatomy. In Great Blue Herons, fine structures of the pecten (Brackevelt 1991), rods and cones (Brackevelt 1994) and cone pigments (Brackevelt and Young 1994) have been studied. Their rod to cone ratio is also documented; it is 0.6:1, which puts them in between the diurnal herons (e.g., the Tricolored Heron, *Egretta tricolor*, has a rod to cone ratio of 0.3:1) and the nocturnal herons (e.g., the Yellow-crowned Night Herons, *Nycticorax violaceus*, has a 2.3:1 rod to cone ratio; Rojas et al. 1999). Generally, higher rod to cone ratios produce better night vision than lower rod to cone ratios (Rojas et al. 1999). In Great Egrets the only scholarly

reference regarding their eye anatomy dates back to a 1917 book, in which the basic macrostructure of the pecten, and the “dominant color” of the fundus were described (Wood 1917).

We were somewhat surprised that our results suggested that herons do not orient themselves to reduce glint and self-shadow in their strike zones. While we have suggested some avenues of study to investigate other potential behavioral or anatomical mechanisms for reducing glint exposure in herons, it is possible that there are cross-media predators that do use body orientation to mitigate effects of glint. There is some anecdotal evidence for this behavior in Brown Pelicans (*Pelecanus occidentalis*) and terns (Carl 1987; Supporting Information). Therefore, we suggest further study of body orientation relative to sun bearing in these, and other, plunge-diving birds.

Lastly, we suggest continuing to use radiative transfer modeling to better understand the light conditions that air-to-water cross-media predators face while foraging. This new tool might also be useful for re-examining work from previous studies, for example on the physical conditions that affect foraging success in piscivorous birds (e.g., Grubb 1977, Bovino and Burt 1979, Carl 1987). Understanding the conditions under which birds view their prey will lead to deeper understanding of their visual and behavioral ecology.



## 1.6 Supplemental Material

- i. Supplemental video of a tern diving repeatedly at 140 degrees to the sun bearing at the Smithsonian Marine Station in Ft. Pierce, FL:  
[https://figshare.com/articles/Tern\\_diving\\_at\\_140\\_deg\\_to\\_sun\\_bearing/5675092](https://figshare.com/articles/Tern_diving_at_140_deg_to_sun_bearing/5675092)
- ii. Data: <https://figshare.com/s/d60a29cbfa5dc77f3fd5>
- iii. R and MATLAB codes: <https://figshare.com/s/215ca91aca66b3c16ea7>

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## **CHAPTER TWO**

### **The physics of air-to-water cross-media predation, and the puzzle of head-tilting in herons**

Collaborators: Margaret Rubega, C. Seabird McKeon, and Anthony Rizzie

## 2.1 Abstract

The behavior of light as it meets an air-water interface creates perceptual challenges for predators who hunt across this interface. The reflection of sunlight from a water surface (glint), can cause visual obstruction (glare), and the bending of sunlight crossing from air to water (refraction) can cause prey to appear to be where they are not. Several diurnal members of the heron clade (Aves: Ardeidae) display a peculiar foraging behavior known as "head-tilting", in which the heron tilts its long neck to one side prior to striking at prey across the air-water interface. A long-standing hypothesis about the significance of head-tilting proposes that it functions to shift sun glint away from the strike zone, allowing the predator to visualize prey more effectively. We formulated a new, alternative hypothesis: that herons align their necks and bills with direct sunlight in a manner that corrects for light refraction (which distorts prey location), by throwing shadows that align with the actual position of prey. We tested both hypotheses empirically by quantifying head orientations of free-living herons prior to, and during head-tilts, as well as during post-head-tilt strikes, using 3D digitization techniques. We used radiative transfer modeling to estimate the amount of sun glint they experienced before and during head-tilts. Head orientations of actively foraging herons are inconsistent with those predicted by both hypotheses, suggesting that cross-media foraging in herons is supported by as-yet unexamined mechanisms. Finally, we propose a third hypothesis for head-tilting: this behavior may allow herons to evade being recognized by fish, by capitalizing on the physics of underwater light transmission, and fish visual systems, to obscure recognition of their heads.

## 2.2 Introduction

There are many visual challenges associated with capturing fish across the air-water interface, including (a) being subjected to sun glint, which is the reflection of direct sunlight from a water surface that can cause glare and obscure the image of submerged prey, (b) having to correct for refraction, which is the bending of light as it crosses media of different densities that causes prey to appear where they are not, and (c) trying to avoid being detected/recognized by prey. Indeed, all cross-media predators must somehow either solve or avoid these challenges. Some predators circumvent the problem of glint by hunting nocturnally (e.g., fishing cats; Cutter et al. 2014), or non-visually (e.g., fishing bats, fishing spiders; Campbell and Suthers 1989, Bleckmann and Barth 1984). Some reduce the need to correct for refraction by aiming strikes more perpendicularly to the water surface with increasing age (e.g., brown pelicans; Carl 1987). Some have wide gapes, which make precise correction for refraction less important (e.g., silver arawanas, Lowry et al. 2005). Some animals evade detection via crypsis (e.g., white-plumaged herons may be more camouflaged against bright skies than darker herons; Green and Leberg 2005). But several herons have a particular problem in that they must deal with all three of these issues – they are visual, mostly diurnal, hunters; they rarely strike perpendicularly to the water surface in the wild; and many species wade in the water, amidst their prey. As the waterbird clade (based on Prum 2015) has had about 50 million years to adapt to these challenges, it would be surprising if they had not evolved physical or behavioral adaptations for them. We know that several avian clades (including waterbirds) have evolved adaptations for intense light directed at them from above; e.g.,



via morphologies such as supraorbital ridges and dark pigmentation near the eyes, which block or absorb sunlight, to reduce its negative visual effects (e.g., Yosef et al. 2012). Therefore, we may also expect to find adaptations for intense light coming from below.

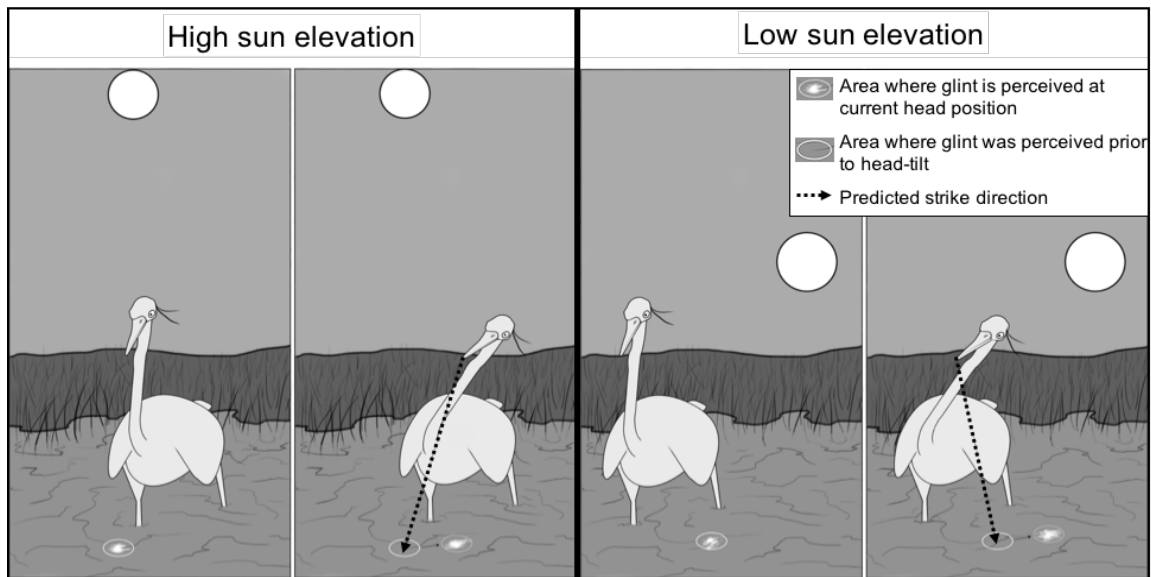
In light of all of the challenges of cross-media foraging, the functional significance of a peculiar-looking behavior called head-tilting (Fig. 1) is of particular interest. Head-tilting by herons was documented by Meyerriecks (1962), and then Krebs and Partridge (1973) noted that during this behavior, Great Blue Herons (*Ardea herodias*) often stand at an angle to the sun, and then tilt their *necks* over to one side. Because they observed that head-tilts were eight times more likely to be directed toward than away from the sun's bearing, and that head-tilts were more common on sunny than cloudy days, they hypothesized that the purpose of head-tilting was to shift sun glint away area toward which they intended to strike. This hypothesis, hereafter referred to as the “glare hypothesis for head-tilting,” seems intuitive; humans also move their heads to shift glint. Demonstrating that herons actually employ head tilting in this way requires us to understand how both position of the bird in relation to the sun, and sun elevation above the horizon, should influence head-tilting behavior.



**Figure 1.** A photo of a head-tilting Great Egret (*Ardea alba*). Note that the entire neck, not just the head, is tilted over to one side.

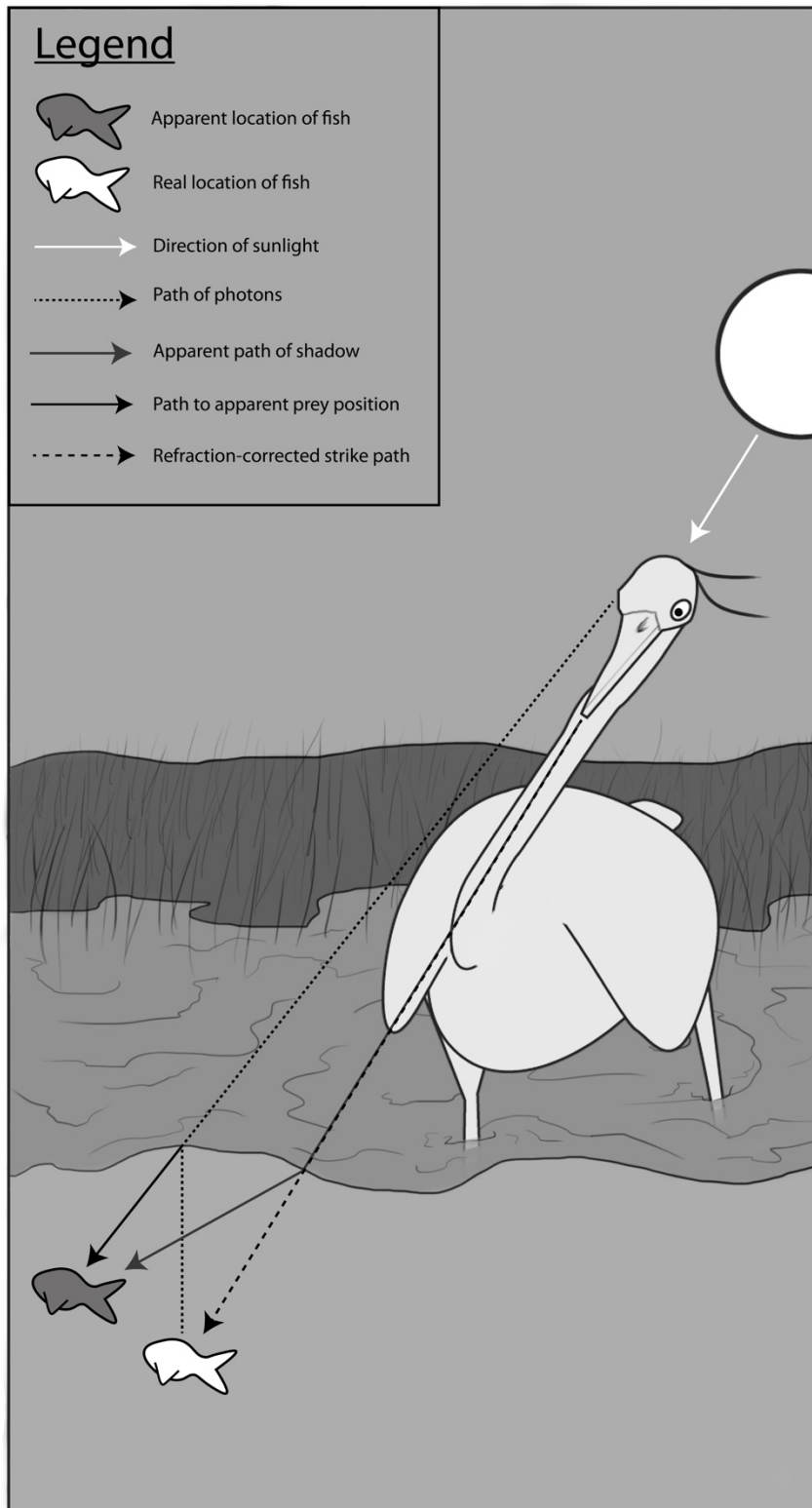
We tested four predictions following from the glare hypothesis for head-tilting, under the assumption that herons orient at an angle to (i.e., neither directly toward or away) the bearing of the sun (based on Krebs and Partridge 1973): 1. Strikes following a head-tilt should be directed toward the area where they perceived glint prior to the head-tilt, and this should be influenced by the position of the sun, because sun position affects the location at which glint is perceived (Fig. 2). Therefore, we predicted that strikes would be aimed in the same direction (i.e., same side of the body) of the head-tilt at the lowest

visible sun elevation angles, and opposite the direction of the head-tilt (i.e., opposite side of the body) at the highest sun elevation angles. 2. We predicted that herons would experience less glint during than prior to a head-tilt. 3. As noted by Krebs and Partridge (1973), herons should not head-tilt when the sun is completely obstructed. 4. Herons should not head-tilt while facing  $180^\circ$  (i.e., directly away) from the sun's bearing, since glint should not factor into foraging under these conditions (Table 1).



**Fig. 2.** Schematic representation of predicted strike directions of herons following head-tilts. Please note that we intend for the sun to be in the foreground of each panel (i.e., in front of the heron). According to previous researchers, herons orient at an angle to the bearing of the sun (i.e., not directly toward or away) while head-tilting. We assumed this to be true in making our predictions. Head-tilting may move glint (shaded white circle) out of the area in which the bird will strike (dotted black arrow). Birds should strike toward the area where the glint appeared before the head-tilt (hollow white circle). Therefore, we predicted that (a) strikes should appear to be directed away from the direction of the head-tilt at high sun elevation, and (b) toward the direction of the head-tilt at low sun elevation.

Glint-avoidance is not the only possible explanation for head-tilting behavior; recall that refraction presents a significant challenge to successful cross-media foraging. We propose here an alternative new hypothesis, that head-tilting enables herons to correct for refraction while striking at prey. Just as a point source of light, such as a laser, can help a person hunting fish with bow and arrow to correct for refraction (Huang 1996), a point shadow could theoretically do the same for a heron. If the bird head-tilts at an angle that aligns the underwater shadow of its long, thin head and bill into a single point shadow over where the prey appears, then its bill will be pointing directly towards the real location of the prey (Fig. 3). In other words, herons could use shadows during head-tilting to create a refraction-corrected “track” along which to strike. This is despite the fact that it will appear, from the heron’s point of view, that it is aiming too low in the water column.



**Fig. 3.** Schematic showing how head-tilting may correct for refraction. The shadow of the bird's head (grey arrow) *appears* to bend outward, from the perspective of the heron. Note that the apparent path of the bird's shadow *does not* describe the actual path of photons, which instead bend downward into the water (dotted line). If the heron can head-tilt at an angle that aligns the underwater shadow of its head and bill into a single point over where the prey appears (dark fish), the angle of its head and bill will instead be aligned between the sun and the real location of the prey (light fish). This would create a refraction-corrected track (dashed arrow) along which to strike.

Under the refraction hypothesis for head-tilting, we predicted that: 1. Herons' heads should be in exact alignment with the sun during head-tilts. Therefore, the difference between the orientations (in 3 dimensions) of the incoming direct sunlight and the heron's head should be approximately zero during the head-tilt, particularly near the end of the pre-strike phase (as defined by Katzir and Intrator 1987). This would easily distinguish the refraction hypothesis from the glare hypothesis for head-tilting; under the latter we would not predict to see this distinctive pattern. 2. Strikes should always be directed away from the direction of the head-tilt, which contrasts with our prediction under the glare hypothesis for head-tilting that under low sun elevations herons should strike in the direction of the head tilt. 3. Herons should still head-tilt while facing directly away from the sun's bearing, since they could still move their heads via head-tilting to align with the direction of sun rays, whereas a heron responding to sun glint should gain no benefit from head tilting while facing away from the sun's bearing.

Under either the glare or refraction hypotheses for head-tilting, a bird striking the wrong way should have reduced foraging success. Additionally, under both hypotheses, the heron's neck should always be directed generally toward the bearing of the sun.

In order to determine whether head-tilting behavior in herons serves as a means of overcoming visual challenges associated with cross-media foraging, we empirically tested the glare and refraction hypotheses for head-tilting in herons via video recordings

of foraging free-living herons under a variety of sun positions and elevations, and quantification of head angle, strike directions, and foraging success.

**Table 1.** Predictions under each of two hypotheses about the functional significance of head-tilting. Bold words = prediction supported by our work; grey words = prediction not supported by our work; grey words in grey boxes = prediction not formally tested by our work.

	Glare Hypothesis	Refraction Hypothesis
<b>1. Direction of strike at low sun elevation:</b>	toward HT	always away from HT
<b>2. Direction of strike at high sun elevation:</b>	away from HT	always away from HT
<b>3. Birds striking "wrong" direction should have lower strike success?</b>	yes	yes
<b>4. Neck orientation during HT:</b>	neck should always tilt toward sun	neck should always tilt toward sun
<b>5. Head alignment during HT:</b>	should not always be in direct alignment with sun	always aligned with direct sun
<b>6. Should HT occur when heron faces away from sun?</b>	no	yes
<b>7. Should HT occur when sun is completely obstructed?</b>	no	no
<b>8. Exposure to glint before vs. during HT:</b>	lower during HT	should not matter
<b>9. Visual signal-to-noise ratio before vs. during HT:</b>	higher during HT	should not matter

## 2.3 Methods

From December 2014 - March 2015, we opportunistically recorded feeding free-living herons (*A. alba*, *A. herodias*, *E. caerulea*, *E. thula*, and *E. tricolor*) along the shoreline of the Indian River Lagoon in Fort Pierce, FL, as well as the western coast of Tavernier, FL, from 3 angles, simultaneously, with high-speed digital video. We similarly recorded free-

living herons at two baited foraging pools. One square, stationary foraging pool (3.66m long x 3.66m wide x 0.31m deep) was located on the property of the Smithsonian Marine Station, in Fort Pierce. The other, small, mobile foraging pool was a standard 34L round pond lining container (66.04 cm in diameter x 17.78 cm deep), which was transported between local fishing piers in Fort Pierce, FL, to take advantage of the fact that herons are known to steal fish from bait buckets. Both pools were stocked with live bait fish (*Opisthonema oglinum*, *Gambusia affinis*, and *Carassius auratus*), and commercially available live shrimp (*Penaeidae spp.*). The identities of prey species in the herons' natural habitats were unknown. All video was taken with the GoPro HERO4™ Silver at 120 frames per second, with 720 pixels of vertical resolution. During each foraging bout, we recorded location (by retrieving latitude and longitude from Google Earth), date and time, which allowed us to retrieve sun position information from the National Oceanic and Atmospheric Administration's online solar calculator (<https://www.esrl.noaa.gov/gmd/grad/solcalc/azel.html>). We also recorded wind speed category (using Beaufort scale), wind direction, cloud cover, and sun visibility, all of which affect levels of sun glint.

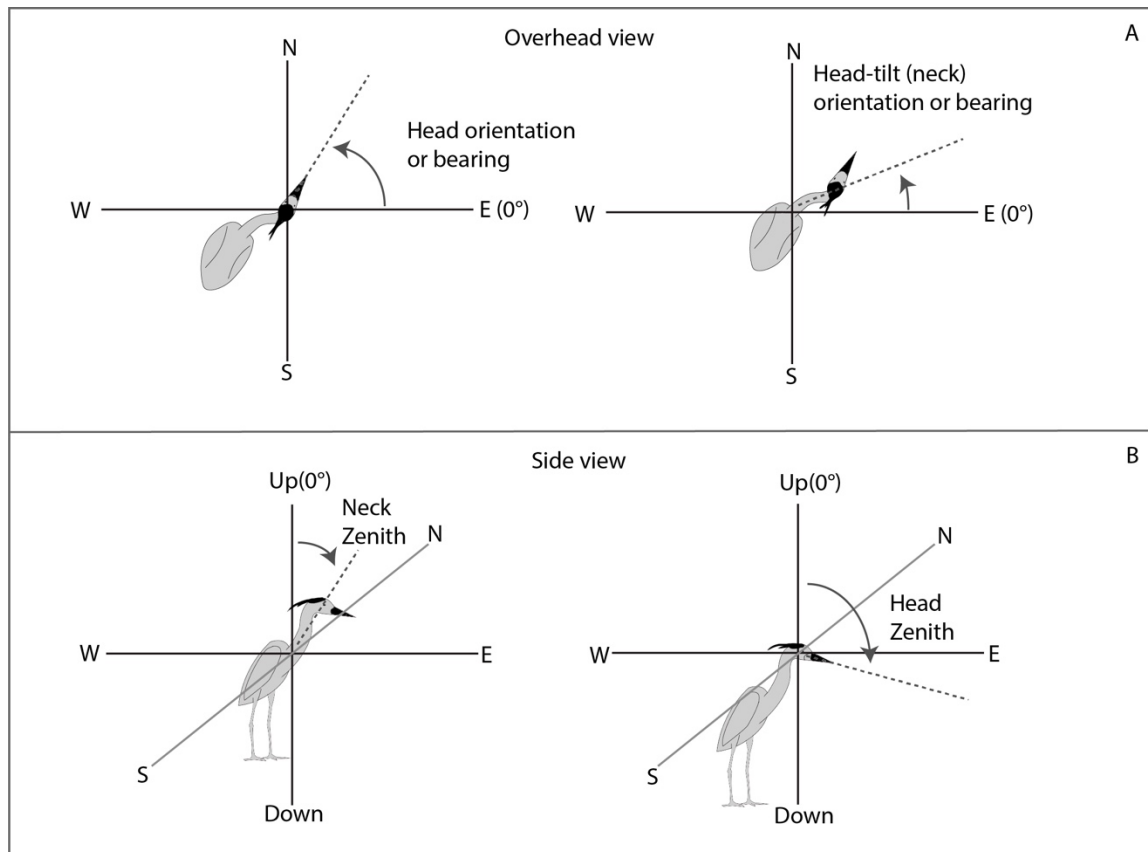
We reviewed footage from 45 two-hour-long sequences of high speed video, and found 60 instances of head-tilting that we were able to see well enough in the videos to be able to digitize (i.e., the head was visible during the complete head-tilt and strike). Birds were unmarked, and thus we can only estimate, given our limited ability to keep track of single individuals, that these instances were from at least 16 individuals. We only digitized



instances where head-tilts were followed by strikes, to be sure that the behavior was related to the heron's foraging ecology, rather than, for example, tilting its neck into strong winds in order to maintain balance.

We calibrated cameras for distance with a program called easyWAND (Theriault et al. 2014) using homemade wands of known length and background points that were visible in each camera view. A small wand, constructed from knitting needles and two Styrofoam balls on each end, was used to calibrate cameras recording at the mobile foraging pool, while a larger wand, constructed from a meter stick and two tennis balls, was used at the stationary foraging pool and in the natural habitats. Camera views were geographically oriented using a clear fish tank (e.g., a right rectangular prism), which was marked on the northeast corner and oriented using a handheld compass so that the long sides of the tank pointed north and south, and the short sides pointed east and west. The transparency of the fish tank allowed for us to be able to see the corners (and thus the geographic orientation) from any camera direction. Using 3D digitizing software, DLTdv5 (Hedrick 2008), we quantified heron head and neck positions in 3-dimensions, relative to geographic north, for each head-tilt/strike pair. We did this once every 10 frames prior to a strike, starting from at least 30 frames prior to the head-tilt where possible. We similarly quantified body positions during the head-tilts. We conducted quality control by excluding 1 video in which error in the locations of digitized points (in 3 dimensions) exceeded 2 pixels in length, possibly due to accidental movement of the camera in the field. We quantified our error by comparing the calculated orientations of

heron heads after HMB and both undergraduate research assistants digitized the same 27 frames (orientation error =  $1.53^\circ \pm 2.36^\circ$ ). We then used our positional data to quantify the 3-dimensional orientations of heron heads, necks, and bodies before and during each of the head-tilts that occurred before a strike (Fig. 4).



**Fig. 4a-b.** Schematic representations of selected measurements. Origins are drawn with respect to the focal body part for ease. Orientation or bearing (a) can be thought of as the direction the bird – or its head (left) or neck (right) – faces, as it would appear from overhead (i.e., in 2 dimensions). Note that 0° bearing on a compass is facing north, and degrees increase as individuals rotate clockwise, while 0° bearing in mathematical terms, is equivalent to east, and increases as individuals rotate counterclockwise. Zenith angles (b) are measured from directly overhead, down to the body part of interest.

Statistical analyses were performed in R (R Core Team 2013). We tested whether herons were head-tilting toward, more often than away, from the sun's bearing, using chi-squared tests. In addition, we compared strike success of birds striking the “right” way versus the “wrong” way (against our predictions), using Fisher's exact tests.

We also compared the degree to which herons head-tilted when the sun was visible versus obstructed using t-tests. In order to do so, we transformed the heron orientation data to quantify the degree of rotation about the body axis during each head-tilt by normalizing the heron's neck position to the position of the heron's body as if we were facing directly toward the front of the bird (Fig 5). To do so, we projected the vector created by the heron's neck ( $\vec{h}$ ) into the vertical plane orthogonal to the direction that the bird's body was facing ( $\vec{d}$ ), and used the new neck direction vector ( $\vec{v}$ ) to describe the rotation of the neck relative to the z-axis (Stewart 2016). Vector  $\vec{h}$ , which points in the direction  $\langle h_1, h_2, h_3 \rangle$ , was defined by two points; the first point was at the eye of the bird, and the second point was given either by the base of the heron's neck, or if that was not visible the kink in the heron's neck at the 6<sup>th</sup> cervical vertebra was used as a proxy for the direction of the base of the neck in relation to the bird's head. If vector  $\vec{d}$  points toward  $\langle a, b, c \rangle$ , the plane onto which we can project  $\vec{h}$  is given by  $ax + by = 0$ . Therefore, the basis of the plane is  $\{ \langle b, a, 0 \rangle, \langle 0, 0, 1 \rangle \}$ , which can be normalized to  $\{ \frac{1}{\sqrt{a^2 + b^2}} \langle -b, a, 0 \rangle, \langle 0, 0, 1 \rangle \}$ . Then a new vector for the heron's neck ( $\vec{v}$ ), which is directed toward  $(v_1, v_2, v_3)$ , can be projected into place as follows:

$$\vec{v} = \left\langle \frac{(-bv_1 + av_2)(-b)}{\sqrt{a^2 + b^2}}, \frac{(-bv_1 + av_2)(a)}{\sqrt{a^2 + b^2}}, h_3 \right\rangle$$

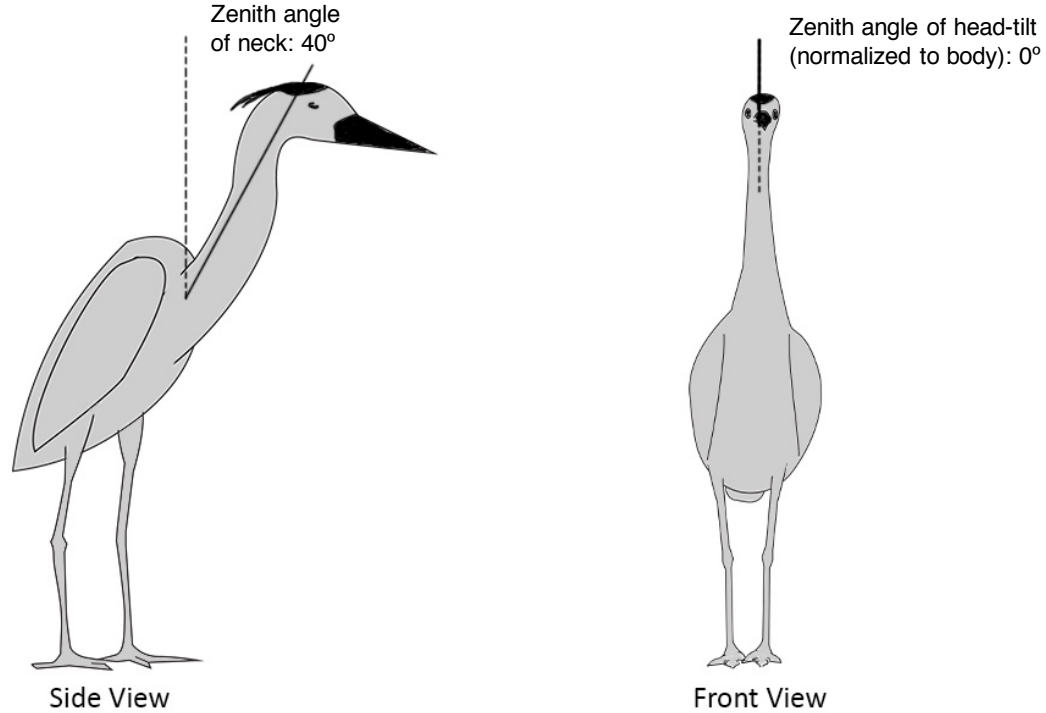
We can now quantify the angle ( $\theta$ ) between vector  $\vec{v}$  and the z-axis, which describes the degree to which the heron is head-tilting, normalized to the direction of the body, using dot products to multiply vectors (Lay 2011):

$$\cos \theta = \frac{\vec{v} \cdot (0,0,1)}{|\vec{v}| \cdot |(0,0,1)|} = \frac{h_3}{|\vec{v}|}$$

and therefore,

$$\theta = \cos^{-1} \frac{h_3}{|\vec{v}|}$$

Normalizing the angle of the head-tilt by the bearing of the body is important because a bird that is not head-tilting at all ( $\theta = 0^\circ$ ) may be holding its neck forward at a zenith angle of  $40^\circ$  (Fig. 5).



**Fig. 5.** A schematic of the same heron from different views, highlighting the importance of normalizing the head-tilt zenith to the orientation of the heron's body ( $\theta$ ) and not using the neck zenith angle as a proxy for the head-tilt zenith.

To test predictions 1 and 2 (Table 1) under the glare hypothesis for head-tilting, we first investigated whether herons were more likely to strike toward the direction of the head-tilt at low sun elevation, and away from the head-tilt at high sun elevation, using binomial generalized linear models. We ran separate models for herons that head-tilted toward versus away from the sun's bearing, as our predictions about strike direction hinged on the expectation that herons would be head-tilting toward the sun the majority of the time.

We then modeled the amount of glint that would be experienced by the herons foraging in their natural habitat (i.e., we excluded observations of herons foraging in baited pools for this analysis), using radiative transfer modeling within the program, Hydrolight (Mobley 1998). As many herons have been shown to have binocular overlap in front of their bills (Martin and Katzir 1994), we assumed that their viewing direction was aligned with the direction of the bill for these models. We estimated proportions of glint ( $L_{sr}$ , or surface-reflected radiance) and radiance upwelling from beneath the water surface ( $L_w$ , or water-leaving radiance) in the green spectrum (550 nm) out of total green radiance ( $L$ ). Following Brown et al. (submitted), we used only green light for this analysis because it tends to penetrate deepest into coastal waters (Kirk 2011), and therefore should be most available to be reflected by the seafloor and exit the water. Therefore, in comparing glint to water-leaving radiance in the green spectrum, we are making conservative estimates of glint. We then calculated the signal to noise ratio, which we defined as the ratio of water-leaving radiance ( $L_w$ ) to glint ( $L_{sr}$ ) in the green spectrum. We also used other conservative but realistic model inputs representing heron foraging conditions in Florida. We used light-colored sand (specifically, ooid sand, which is typical in the area) and a medium value for light attenuation (i.e., light attenuating by half for every meter below the sea surface; McPherson et al. 2011). We also used a water depth of 28 cm to reflect estimates of heron foraging depths in the literature (Powell 1987; Bancroft, Gawlik & Rutchey 2002), and ran the model under two wind conditions (5 m/s, and 10 m/s) and two sunlight conditions (visible sun, obstructed sun). We then extracted output values from the model for glint and water-leaving radiance, based on an average orientation using the

first three digitized frames prior to each head-tilt and the three frames during the most extreme portions of each head-tilt, and compared these pre-head-tilt and head-tilt values with paired t-tests.

Lastly, to test the refraction hypothesis for head-tilting, we calculated the total angle (in 3 dimensions) between the direction of direct incoming sunlight, and the herons' heads during pre-head-tilt frames, head-tilts and strikes. We can call the orientation of the heron's head (or any other body part)  $\alpha$ , and again then use the dot product formula to find the value of  $\alpha$  (Lay 2011). The formula is as follows:

$$\cos \alpha = \frac{\vec{h} \cdot \vec{s}}{|\vec{h}| \cdot |\vec{s}|},$$

where  $\vec{h}$  is the 3D vector pointing from the origin of a graph toward position  $\langle h_1, h_2, h_3 \rangle$ , the direction of which is defined, in this case, by the direction of the bill relative to the eye of the bird, and  $\vec{s}$  is the vector describing the direction of the sun. Because we were only interested in the direction of the sun in relation to the heron, and not the length of the sun's ray, we used a vector of length 1 for simplicity in the calculation. Therefore, this equation can be simplified to:

$$\cos \alpha = \frac{\vec{h} \cdot \vec{s}}{|\vec{h}|},$$

or:

$$\cos \alpha = \frac{h_1(\cos \theta \sin \varphi) + h_2(\sin \theta \sin \varphi) + h_3 \cos \theta}{\sqrt{(h_1)^2 + (h_2)^2 + (h_3)^2}}$$

The angles theta ( $\theta$ ) and phi ( $\varphi$ ) appearing in the formula come from the spherical coordinate description of the vector. (The third spherical coordinate, rho or  $\rho$ , would signify the length of the vector of the sun's ray, and does not appear as we used a value of 1.)

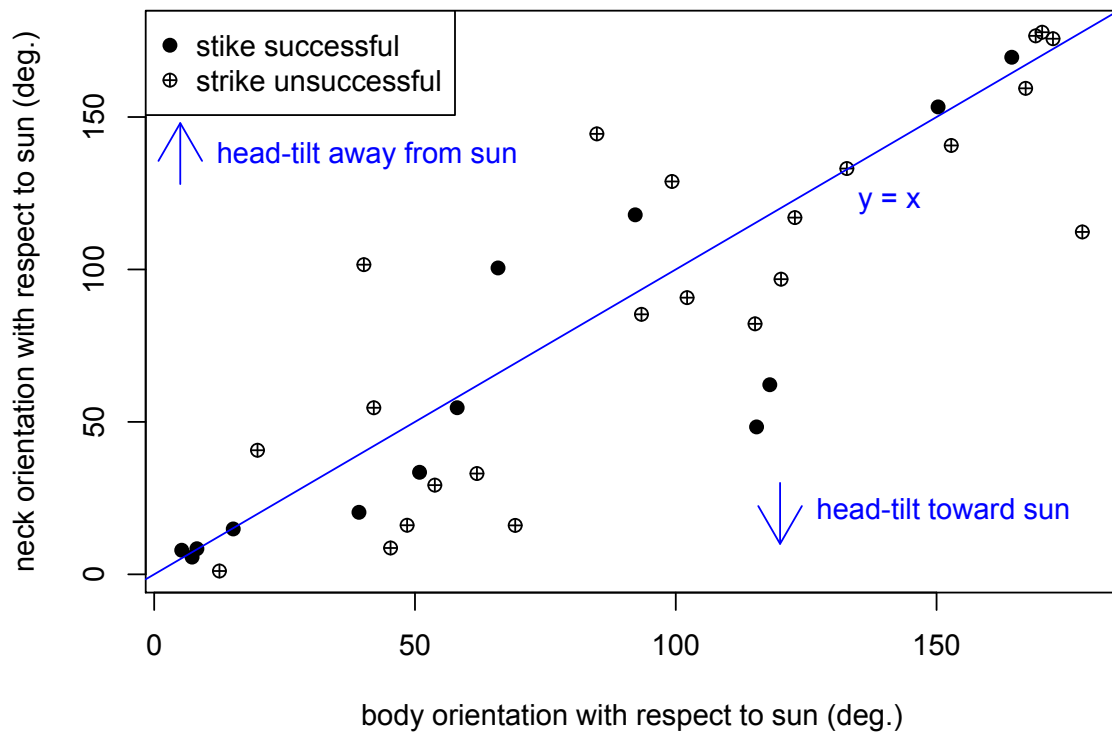
We then tested whether the heads were aligned with the direction of the sun using regression with generalized estimating equations to account for the fact that there were multiple frames digitized for each individual, and intra-individual measurements are not independent (Supplemental Material).

## **2.4 Results**

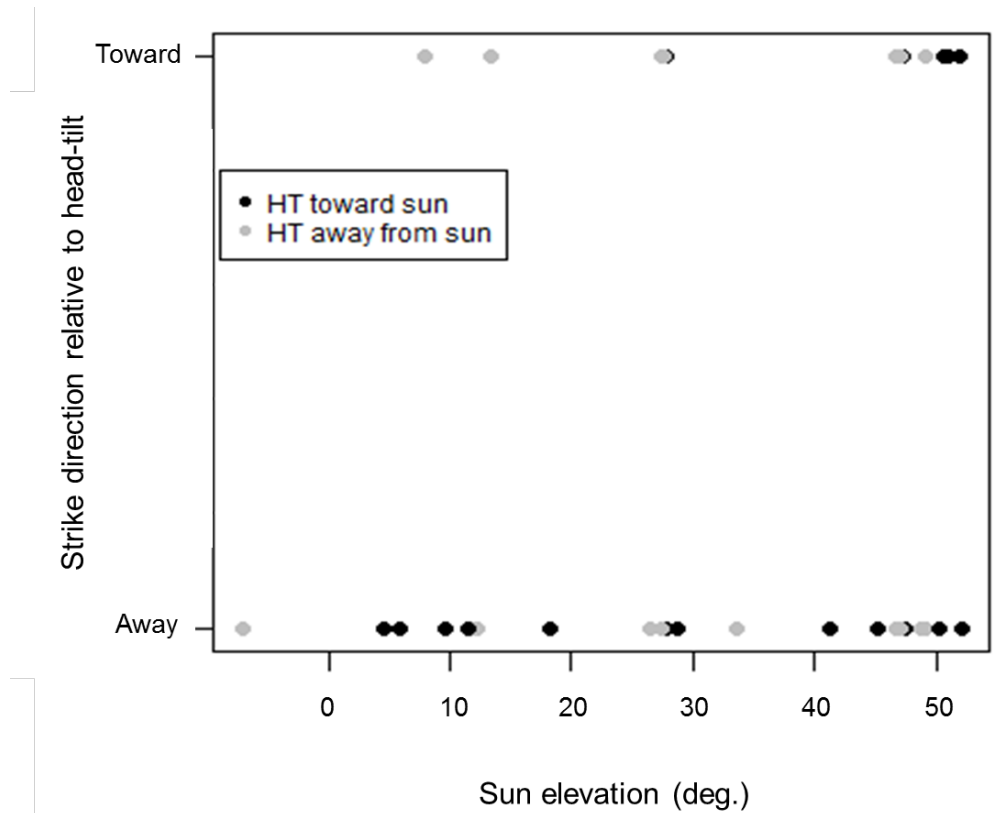
Neither of the two hypotheses we tested as explanations for head-tilting in herons was supported by our research. Data from our video analysis contradicted the two main predictions of the first hypothesis, the glare hypothesis for head-tilting. Our sample of herons only head-tilted toward the sun by a factor of less than 3 to 1, both when data from natural habitats and foraging pools were pooled (chi-sq. = 15.34, df = 1, n = 71, p < 0.0001), and when using natural habitat alone (chi-sq. = 9.31, df = 1, n = 52, p = 0.002) (Fig. 6). Even when we based our models on only those case where herons head-tilted toward the sun, our predictions about where herons would strike following a head-tilt did



not hold ( $z = 1.45$ ,  $df = 31$ ,  $p = 0.15$ ; Fig. 7). Furthermore, herons still head-tilted even while facing almost directly away from the sun's bearing (Fig. 6), and did not suffer reduced foraging success for striking away from the predicted direction ( $p = 1.0$ ). At low ( $<45^\circ$ ) sun elevations, 12 of 23 head-tilts were in the expected direction (toward the sun), and only 1 struck in the expected direction (toward the head-tilt). That strike was unsuccessful. At high ( $>45^\circ$ ) sun elevations, 14 of 29 head-tilts were in the expected direction (toward the sun), and only 9 struck in the expected direction (away from the head-tilt). Of these strikes, 4 were successful, 4 were unsuccessful, and in one case success couldn't be determined from our video. Thus, birds who head-tilted and struck as expected, according to our predictions, had 44% capture success. Birds who struck away from the expected direction had 40.7% strike success (11 successful strikes out of 27 strike attempts).

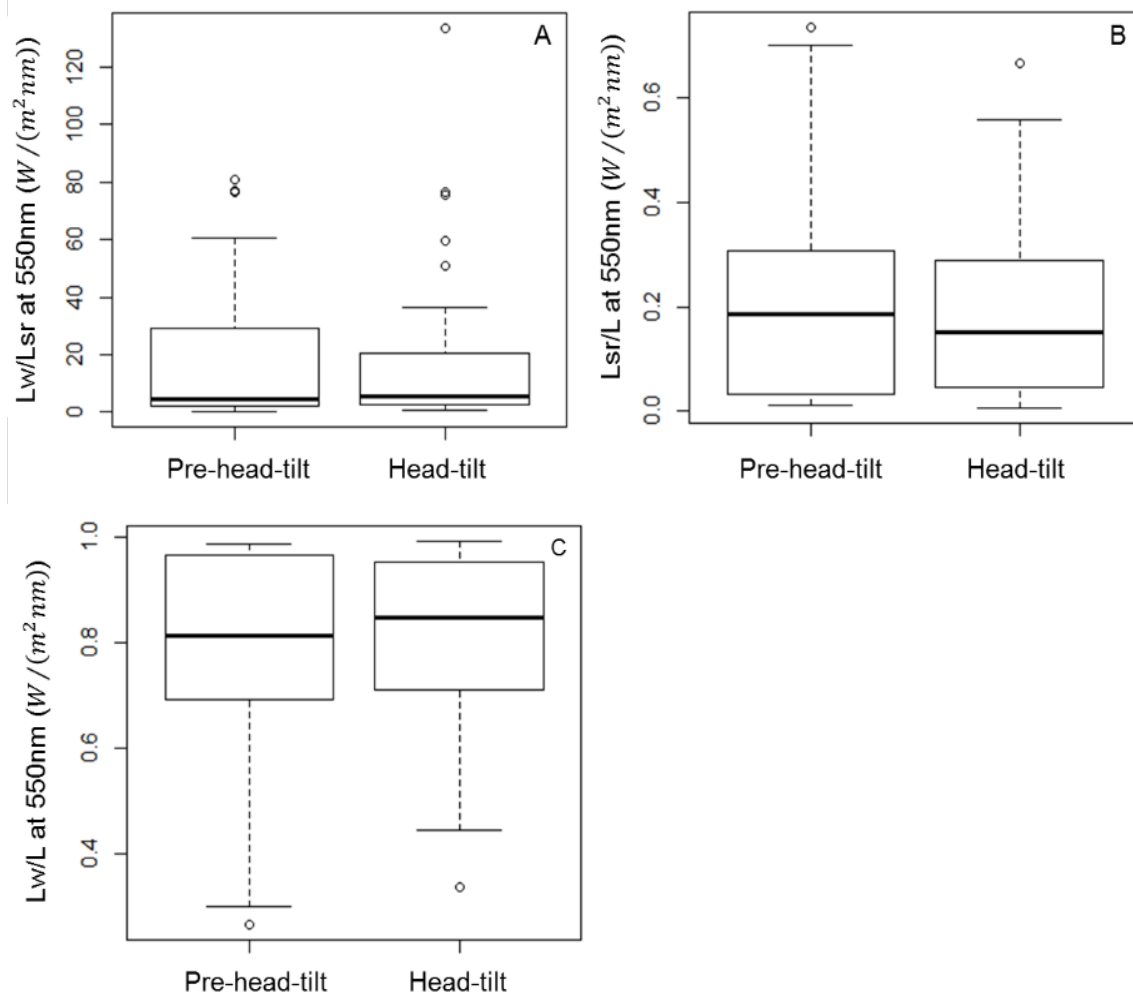


**Fig. 6.** The orientation of the neck during a head-tilt (“HT”) with respect to the sun versus heron body orientation (with respect to the sun) for herons foraging in their natural environment. The blue line represents where the body and the neck of the heron would be facing the same direction. Points below this line indicate that the heron was head-tilting toward the sun, and points above the line indicate that the heron was head-tilting away from the sun’s bearing. Variance among the degrees of tilt contribute to the spread of data points; those which appear to fall on the line are birds which barely tilted. Note that herons still head-tilted when their bodies were oriented almost 180° to the sun. Also note that there was no difference in strike success no matter the direction in which herons tilted their heads relative to the sun ( $p = 1.0$ ).



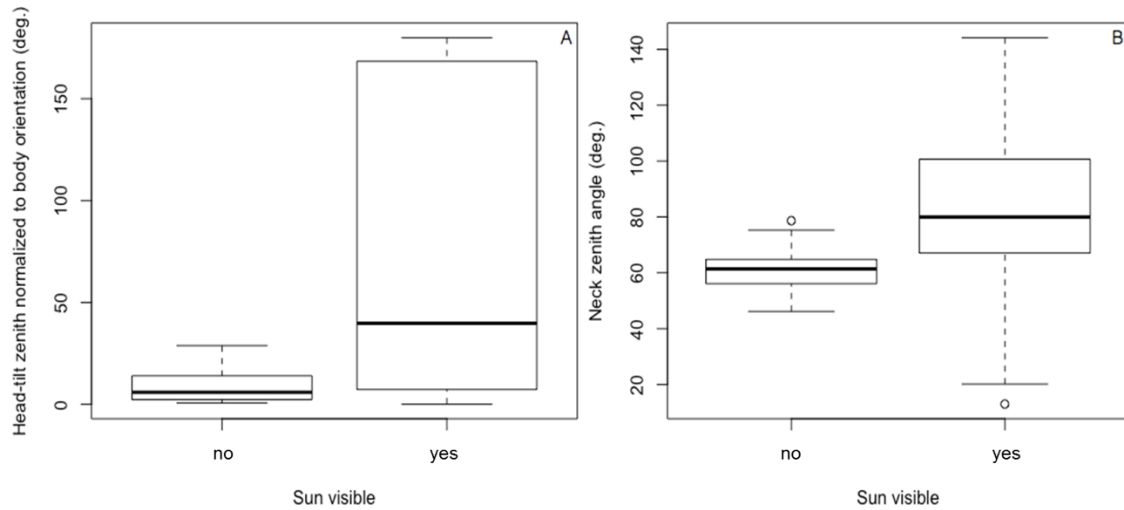
**Fig. 7.** Graph of herons' strikes directed toward or away from the head-tilt ("HT") by sun elevation, and by relative direction of the head-tilt prior to the strike. Note that there is no clear (or statistically significant) pattern in which way the heron strikes following a head-tilt, even when it is head-tilting toward the bearing of the sun (black circles). This is inconsistent with our predictions.

Finally, in contrast to predictions of the glare hypothesis, we found no statistically significant differences in measures of the signal-to-noise ratios ( $t = 1.05$ ,  $df = 28$ ,  $p = 0.30$ ), proportions of water-leaving radiance ( $t = -0.43$ ,  $df = 28$ ,  $p = 0.67$ ) or proportions of glint ( $t = 0.43$ ,  $df = 28$ ,  $p = 0.67$ ) before and during head-tilts, in natural habitats (Fig. 8).



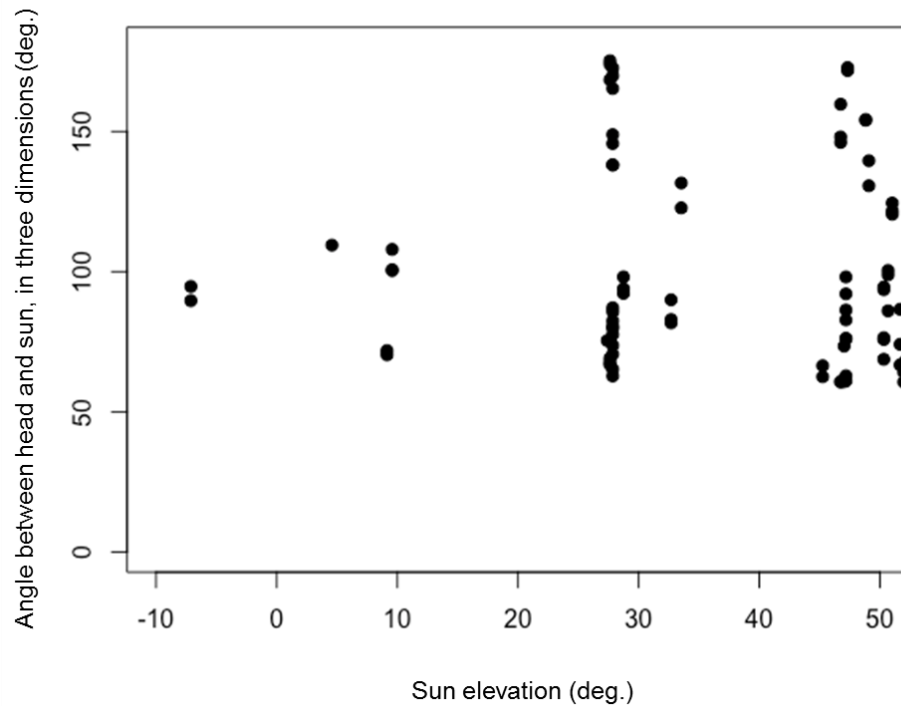
**Fig. 8a-c.** In multiple measures of visibility, including signal-to-noise ratio (a), proportion of glint (b) and proportion of water-leaving radiance (c), there was no difference before and during head-tilts by foraging herons.

Some of our results *were* consistent with predictions for the glare hypothesis. For instance, herons head-tilted farther to the side when the sun was visible than when the sun was obstructed ( $df = 49$ ,  $F=5.63$ ,  $p = 0.02$ ; Fig. 9.), and we encountered few instances of head-tilting when the sun was obstructed as herons foraged in their natural habitats.



**Fig. 9a-b.** Herons head-tilt more extremely when the sun is visible versus obstructed, both in terms of how far they tilt, (a) normalized to axis of the body ( $df = 49$ ,  $F=5.63$ ,  $p = 0.02$ ), and (b) their neck zenith ( $df = 50$ ,  $F = 4.40$ ,  $p = 0.04$ ).

Lastly, in contrast to expectations under the refraction hypothesis for head-tilting, we found that the angle at which herons orient to the sun's bearing is about  $105.79^\circ \pm 13.39^\circ$  (clusters = 34, Wald statistic = 62.45,  $p < 0.0001$ , Fig. 10) across all sun elevations (i.e., the slope for sun elevation was  $-0.15^\circ \pm 0.32^\circ$ ; clusters = 34, Wald statistic = 0.22,  $p = 0.64$ ). Therefore, since the herons never align their heads with the sun, they cannot create a refraction-corrected track using the shadows of their heads and bills. Further, strikes were not always directed away from the direction of the head-tilt, as was also predicted under this hypothesis.



**Fig. 10.** Scatterplot of the angular difference between the orientation of the herons' heads and the direction of incoming sunlight, across all sun elevations. If the refraction hypothesis for head-tilting were supported, we would expect all data points to plot along the line  $y = 0$ . That is not the pattern we see here. Rather, herons are never aligning their heads with the direction of direct sunlight.

## 2.5 Discussion

With technological advances that previous researchers did not have access to, such as high-speed videography, 3-dimensional digitizing methods, and radiative transfer modeling programs, we were able to provide strong evidence that herons are not head-tilting to avoid glint or correct for refraction while hunting (Table 1).

Several lines of evidence increase our confidence that head-tilting does not serve to compensate for glint. Under the glare hypothesis for head-tilting, we predicted that if herons were indeed head-tilting toward the sun, then their strikes should be directed toward the head-tilt at low sun elevation, and opposite the head-tilt at high sun elevation. We found no support for this prediction. Moreover, we did not find any statistically significant differences in estimates of herons' exposure to glint before and during a head-tilt. Herons also head-tilted away from the bearing of the sun about 25% of the time, which should never occur if head-tilting serves to compensate for glint. Lastly, herons head-tilted when glint should not have played a significant role in foraging (e.g., while facing almost directly away from the bearing of the sun in Fig. 4; while the sun was below the horizon in Fig. 7; and while the sun was obstructed in Fig. 9). In the one case where we captured a Great Blue Heron head-tilting on video when the sun was 7° below the horizon, it head-tilted in the general direction of a street lamp, but the lamp was not overhead, so we would predict that the bird would be more likely to strike toward the direction of the head-tilt in that case, and that appeared opposite to what occurred (Supplemental Material).

Some aspects of our data *are* consistent with the glare hypothesis; for instance, we found very few occurrences of head-tilting when the heron was facing directly toward the sun. However, we would have expected none. We also recorded very few instances of head-tilting when the sun was obstructed; again, we would have expected none (however, our sample of cloudy days during field work was very small).

Our refraction hypothesis for head-tilting leads to the prediction that herons' heads should be in direct alignment with incoming direct sunlight during the head-tilt. In a sample of 60 strikes following head-tilts, no heron ever aligned its head directly with the incoming sunlight. Therefore, herons could not have been aligning the underwater shadows of their heads and bills with prey to create a refraction-correcting path along which to strike. Do, however, note that we may have found a pattern suggesting that herons are trying to keep their shadows away from fish by keeping their heads out of alignment with the sun (Fig. 10). This could also help to explain why head-tilting occurs more often when the sun is visible.

Our results, by ruling out both the long-standing glare hypothesis and our refraction hypothesis, beg the question: what is the function of head-tilting? There are similar behaviors in other waterbirds; van den Hout and Martin (2011) hypothesized that extreme head-tilting in shorebirds might function as a way for birds to align direct, harmful sunlight onto the pecten at the back of their eye while foraging. The pecten, which provides oxygen and nutrient exchange for the avian retina (Wingstrand and Munk 1965, Pettigrew et al. 1990), is a deeply pigmented organ that protrudes from the optic nerve into the vitreous humor (Wood 1917, Walls 1942), and thus it could possibly serve to absorb light. However, herons are head-tilting at almost all bearings relative to the sun,



including while facing away from the sun's bearing when direct sunlight would not affect the retina.

In light of evidence that suggests that these three hypotheses about the functional significance of head-tilting in herons are unlikely, we propose an additional alternative hypothesis that is consistent with the findings of this study: head-tilting may be a mechanism by which herons avoid being detected or recognized, either by: a. keeping their shadows away from fish, b. exploiting properties of refraction (i.e., Snell's Window) to "hide" from fish in the most distorted areas of the field of view of a fish, or c. both.

Predator-prey interactions are one of the driving forces of natural selection, and thus organisms should evolve to become more efficient in these interactions. For example, both predators and prey should evolve mechanisms that allow them to compensate for challenges that make the other harder to detect. Therefore, predator-prey systems afford us opportunities to study how animals have adapted – behaviorally, morphologically, or physiologically – to overcome these challenges. Here we have tested and rejected two hypotheses, and proposed a third hypothesis, about a behavior which is believed to be involved in compensating for some of these challenges while hunting from air to water, which is a context that is not yet well-represented in scientific literature.

## 2.6 Supplemental Material

- i. Supplemental video of a heron head-tilting past sunset can be found at:

<https://figshare.com/s/d95b3649755fe24e9938>

- ii. Our data files can be found at:

- a. <https://figshare.com/s/eccfdc8967d078fb7205>

- b. <https://figshare.com/s/770bcc8b3fb0e9421d69>

- iii. Our R codes for statistical analyses can be found at:

<https://figshare.com/s/942387f507f0dd03720c>

## 2.7 Acknowledgements

The Link Foundation and Smithsonian Institution awarded a 3-month fellowship to HMB, allowing her to work out of Fort Pierce Marine Station in order to collect video of foraging herons. HMB was also supported by a Crandall-Cordero Fellowship through the University of Connecticut. The Department of Ecology and Evolutionary Biology also awarded a grant to HMB to travel to T. Hedrick' lab at University of North Carolina at Chapel Hill, to learn skills for three-dimensional digitization. The Ornithology Lab members at the University of Connecticut, as well as HMB's dissertation committee members, E. Schultz, E. Adams, A. Moiseff, and H. Dierssen made very helpful comments. H. Dierssen taught HMB how to use Hydrolight to run radiative transfer models, and E. Adams consulted with us regarding statistical analyses. HMB's undergraduate research assistants, M. Mather and K. Struth, tirelessly digitized several

thousands of video frames of foraging herons. B. Cruz contributed illustrations for figures 2-5. W. Lee built the flow-through foraging pool at the Smithsonian Marine Station.

## **2.8 Animal Care Statement**

The University of Connecticut IACUC approved a reciprocity agreement with the Smithsonian ACUC (NMNH-2014-12). The work with free-living herons, and bait fish, was performed under a permit through the Florida Fish and Wildlife Conservation Commission (Permit # LSSC-14-00061).

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## **CHAPTER THREE**

**The functional significance of head-tilting: evading prey visual systems  
in an arms race at the edge of Snell's Window?**

Collaborators: Margaret Rubega, Anthony Rizzie

### **3.1 Abstract**

Hérons, a group of predatory wading birds, have been known to tilt their long necks about the long axis of their bodies while they hunt. The long-standing hypothesis that this behavior mitigated sun glint was inconsistent with findings from our previous work. Therefore, we tested a new, alternative hypothesis, that this behavior helped herons to evade being detected or recognized by their submerged prey. We exposed predator-naïve brown trout to a heron decoy with an upright neck, the same heron decoy with a tilted neck, and to a control condition. We predicted that if our hypothesis were supported, fish exposed to a heron decoy with a tilted neck would exhibit reduced flight behavior as compared with fish exposed to a heron decoy with an upright neck. This prediction was upheld. When controlling for group size, brown trout fled farthest in response to the heron decoy with the upright neck; flight distances when exposed to the decoy with the tilted neck were not statistically different from the control treatment. However, we did not find any difference in how quickly the fish fled from the decoy among treatments. As we used predator-naïve fish in these experiments, we expect that results from predator-exposed fish would yield more exaggerated results, and suggest that this work be pursued.

### **3.2 Introduction**

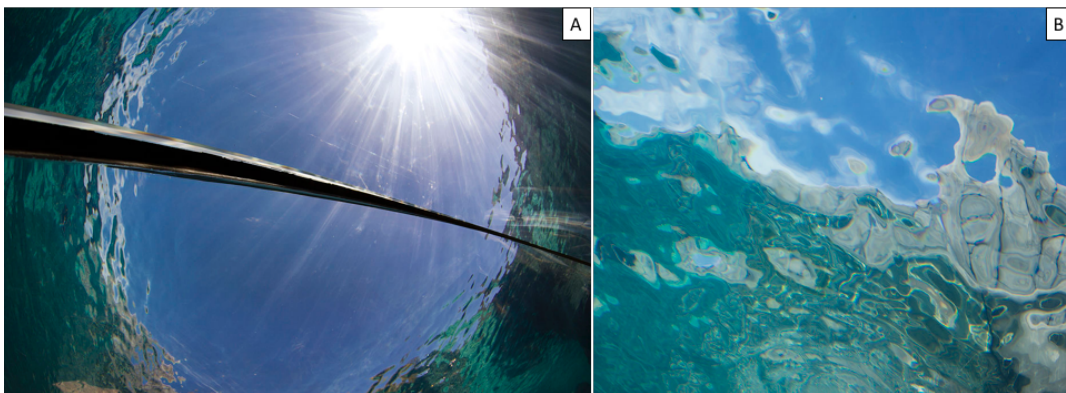
Predators can evade the sensory systems of prey by avoiding detection or recognition (Brown et al. 2006). There are several strategies for doing so, including hiding, having



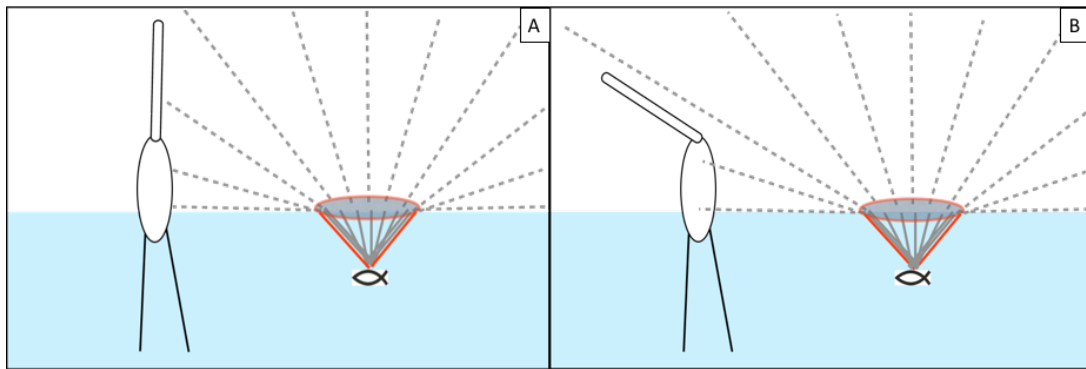
cryptic coloration, engaging in motion camouflage, and masquerading (Stevens and Merilaita 2009). It has also been suggested that predators may be able to avoid detection during cross-media hunting by positioning themselves visually at the edge of Snell's Window, from the perspective of submerged prey (Lotem et al. 1991, Day et al. 2016). However, this hypothesis has not been formally tested. In this study, we tested a hypothesis about how one group of birds, herons, may use Snell's Window to their advantage while hunting.

Herons have long been observed performing a peculiar-looking behavior called head-tilting (Meyerriecks 1962), in which they tilt their long necks out to one side, and then strike sideways, usually opposite to the direction of the head-tilt (refer to chapter 2), at an acute angle to the water surface. Head-tilting was thought to allow a heron to shift a perceived area of sun glint, away from its strike zone (Krebs and Partridge 1973). However, evidence does not support that hypothesis. For example, when using optical models, we found no evidence that herons experience a statistically significant reduction in visual exposure to sun glint before a head-tilt compared to during a head-tilt (refer to chapter 2). Here, we test an alternative hypothesis for head-tilting: rather than aiding in the heron's ability to see, head-tilting may instead aid herons by helping them to remain unseen or unrecognized by prey.

Snell's Window is a physical phenomenon caused by refraction of light. Refraction, or bending of light, occurs when light travels through media of different densities. When light enters the water, it bends downward, causing a viewer in the water to look up and only see a circular window through the air-water interface (Fig. 1). This is a  $97^\circ$  conical window, into which incoming light from  $180^\circ$  of the terrestrial hemisphere is compressed; images outside of the perimeter of this window appear darker, and are an internal reflection of the dimmer aquatic environment (Fig. 1; Kirk 2011). The edge of Snell's Window appears far more distorted than the center. This is because light coming from directly overhead, exactly perpendicular to the water surface, does not bend – it is already coming into the water as “downward” as possible. But all other light coming in is bent at progressively greater angles (refer to equation for Snell's Law, below), as light reaches the water surface from increasingly acute angles. Thus, if herons struck at more acute angles to the water surface, the most “predator-shaped” body parts (their bills) would appear more distorted from the perspective of a fish (Fig. 2).



**Fig. 1. A.** An image of Snell’s Window from an underwater tunnel at the St. Louis Zoo. The dark arc bisecting the image is the junction between two panes of curved glass in the tunnel. Note that the darker area beyond the edge of Snell’s Window shows an internal reflection of the aquatic environment. **B.** A close-up of the edge of Snell's Window, showing the distortion of light and image created by the bending of light as it enters the water. Photo credit: Wikimedia user “Hellbus”, under Creative Commons License BY-SA 3.0 B.



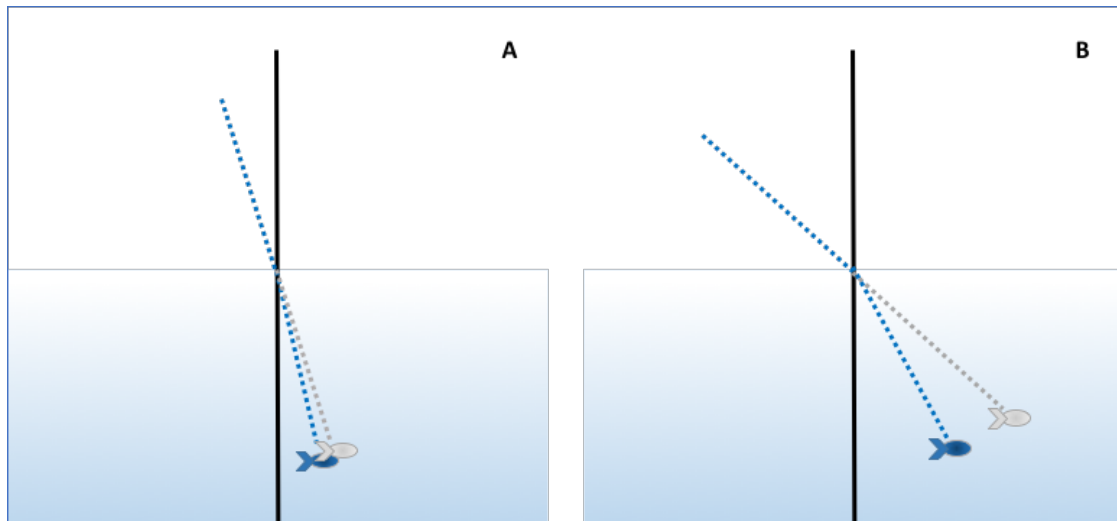
**Fig. 2. A.** The heron can easily be seen by submerged prey prior to head-tilting. **B.** The heron should theoretically be harder to see at edge of Snell’s Window from the perspective of a fish.

The angle of refraction of light traveling from air to water can be found by solving for  $\theta_r$  in the equation for Snell’s Law:

$$1.00 \sin \theta_i = 1.33 \sin \theta_r,$$

where  $\theta_i$  is the angle of incidence with respect to vertical,  $\theta_r$  is the angle of refraction from the water surface with respect to vertical (refer to figure 3), 1.00 is the refractive index of air, and 1.33 is the refractive index of water. The refractive index of water is affected by factors that affect water density (e.g., temperature, salinity), and by the wavelength of light passing through (Mobley 1994). Even still, the refractive index of water ranges from only about 1.329 to 1.367 (Austin and Halikas 1976).

From the perspective of the predator, it might be visually advantageous to strike at submerged prey from more perpendicular angles to the water surface, as there would be less refraction to correct for in a perpendicular rather than an acute angle (Fig. 3). For example, from Snell's Law, we can estimate that if a cross-media predator peers through the water surface toward the apparent location of a fish at an angle of  $10^\circ$  from vertical (i.e., close to perpendicular to the water surface), the difference between where the fish appears (also  $10^\circ$  to the vertical), and where the fish is ( $7.5^\circ$  to the vertical), is only  $2.5^\circ$ . This should be easier to correct for than striking from  $45^\circ$  to the vertical, where the difference between where the fish appears ( $45^\circ$  to the vertical) and where the fish is ( $32^\circ$  to the vertical) is  $13^\circ$ .



**Fig. 3.** A schematic figure, illustrating that **A.** smaller angles of incidence (and smaller viewing angles) with respect to the vertical distort apparent prey position less than **B.** larger angles of incidence with respect to the vertical. The black lines are vertical. The blue dotted lines represent paths of light between a viewer and the real location of the prey (blue fish). The grey dotted line extends from the viewing angle to the apparent location of the fish (grey fish).

While striking from more perpendicular rather than acute angles to the water surface reduces visual distortion of prey location from the perspective of the predator, a consequence of this is that visual distortion of the predator, from the perspective of the prey, is also reduced. When the predator is peering down from directly overhead from the perspective of a fish, its image is directly in the center of Snell's Window, and that fish

will have a clear view of the predator. Therefore, any visual advantage (e.g., reduced refraction angles, reduced visual distortion) that the predator may have when peering straight downward might be negated by its own increased detectability. As prey can flee when they detect predators, there should be strong selective pressure for avoiding detection. It might be especially difficult for a predator that wades amidst its own prey, to avoid being detected or recognized. Thus, it seems likely that a wading predator would gain an advantage by having behavioral and morphological adaptations that allow it to easily keep its most predatory-looking parts (e.g. in the case of a heron, its head and bill) toward the visually distorted edge of Snell's Window while hunting.

There is already some anecdotal evidence that herons might be using visual properties of Snell's Window (from the perspective of the prey) to their advantage. In the field, where prey were unrestrained, herons struck from more acute angles to the water surface (Lotem et al. 1991), than in laboratory settings, where herons struck at confined prey at more perpendicular angles to the water surface (Katzir et al. 1989). In addition, some fish have retinal regions that seem to be specialized for visualizing the edges of Snell's Window, suggesting the possibility of a predator-prey arms race at the edge of Snell's Window (Pitcher 1993).

If herons head-tilt to avoid being detected or recognized as predators while hunting prey through the air-water interface, then fish should have reduced flight responses when

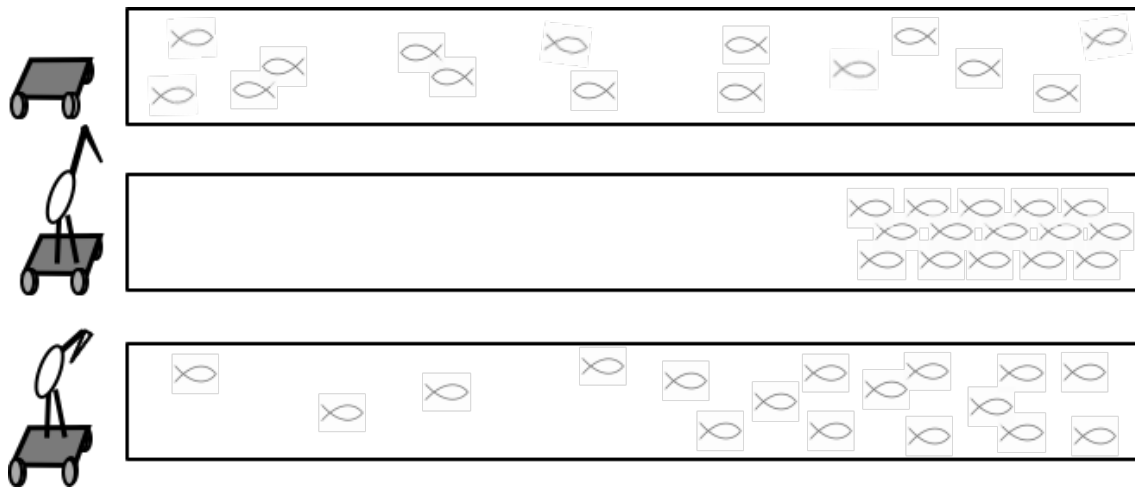
exposed to a head-tilting heron versus a heron with an upright neck. We tested this prediction by exposing predator-naïve Brown Trout (*Salmo trutta*) to a roboticized heron decoy placed in either a head-tilted or upright neck position, as well as a control with no heron decoy mounted. We predicted that, if head-tilting reduces detection or recognition of the predator, then prey would flee shorter distances and more slowly from a head-tilted heron decoy than from a one with an upright neck position. We also expected that these responses might be affected not only by experimental treatment, but also by group size. Groups have a greater chance of detecting a nearby predator as group size increases, and individual risk decreases as group size increases (Pitcher 1993). Therefore, we expected lone fish, which may be most vulnerable, to quickly flee to join up with other fish (Hemelrijk and Hildenbrandt 2007; Hemelrijk and Hildenbrandt 2012), whereas we expected fish in larger groups to have a reduced response in comparison.

Alternatively, if head-tilting does not reduce detection or recognition of the predator, we predicted fish would flee the same distance and at the same speed from the head-tilting decoy as from a decoy with an upright neck. In either case, we did not expect to see flight behavior in response to the control treatment.

### **3.3 Methods**

To test our predictions based on the hypothesis that herons head-tilt to evade being detected or recognized by prey (Fig. 4), we documented fish responses to a life-sized,

robotic great blue heron decoy in head-tilting and upright neck positions, as well as to a control, at a Connecticut State fish hatchery in Burlington, CT, USA, from May 23 – June 17, 2016. All fish care was performed by the hatchery staff, according to their regular maintenance schedules.



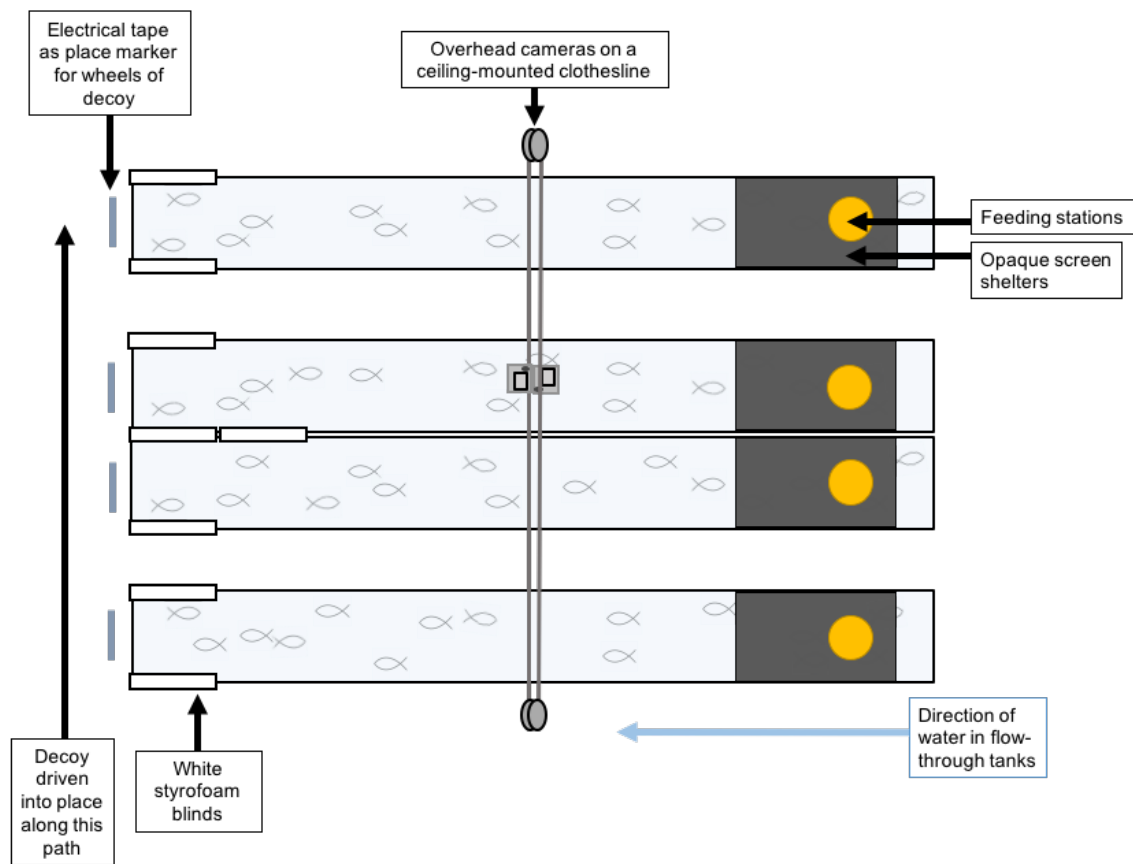
**Fig. 4.** A schematic of our predictions based on the hypothesis that herons head-tilt to evade being detected or recognized by prey. The figures represent overhead views of fish raceways. **Top:** In the control treatment, we presented the crawler with the attached lift (represented by the grey square on wheels). We predicted that fish would not exhibit flight responses in relation to the control. **Middle:** When the decoy's neck was upright, we predicted that fish would flee farther and faster from the decoy, as compared with head-tilting or control treatments. **Bottom:** When the neck of the heron decoy was placed in a head-tilting position, we predicted that fish would flee more slowly and less far, as compared with the other treatments, or that there would be no difference between the responses of fish in the head-tilting and control treatments.

We used 4 indoor raceways, each housing approximately 7,700 predator-naïve brown trout. The water temperature was between 8.9 and 10.0 °C for the duration of the study. The hatchery's overhead fluorescent lights were always on during trials. Raceways were



approximately 7.16m x 0.89m x 0.71m. One side of the raceway was covered with opaque screens under which fish could take shelter (refer to Fig. 5). Therefore, we presented the heron decoys and the control from the opposite side of the raceway.

To build our robotic heron decoy, we first purchased a plastic great blue heron lawn ornament, cut off the neck, and then mounted the two sides of the decoy onto wooden boards that had been cut to fit neatly in between those two sides (Fig. 6). We then adjoined these boards with a spring so that we could tilt the neck sideways, about the long axis of the body; the spring was tight enough to remain in place once placed upright or in a head-tilt position. We mounted the decoy onto a lift platform that was built from PVC piping and a winch kit. We then mounted the platform atop a remotely controlled Redcat Everest10™ electronic crawler (1/10 scale model). For the control treatment, we detached the heron decoy from the crawler.



**Fig. 5.** The physical experimental set-up at the Burlington Trout Hatchery.



**Fig. 6.** A picture of the heron decoy after being cut into two pieces at the base of the neck. The white arrows point to the locations at which we affixed wooden boards to both pieces of the heron decoy. We had these boards cut to the shape of the holes by the University of Connecticut's Technical Services Department. We attached the boards (and thus the two pieces of the heron decoy) together with a spring that allowed the head to swivel.

In order to establish a biologically-relevant standard for the degree to which the robotic heron decoy head-tilted, we quantified the degree to which herons head-tilted in the field. We used a program called DLTdv5 (Hedrick 2008, Theriault et al 2014) to reconstruct 27 head-tilts, in three dimensions, from previous recordings of free-living, foraging tricolored herons (*Egretta tricolor*; at least 2 individuals), snowy egrets (*Egretta thula*; 1 individual) and great egrets (*Ardea alba*; 1 individual). To calculate the degree of head-tilt, we quantified the degree of rotation of the neck about the long axis of each heron's

body, as compared to vertical, using the dot product formula (Lay 2011; also refer to chapter 2):

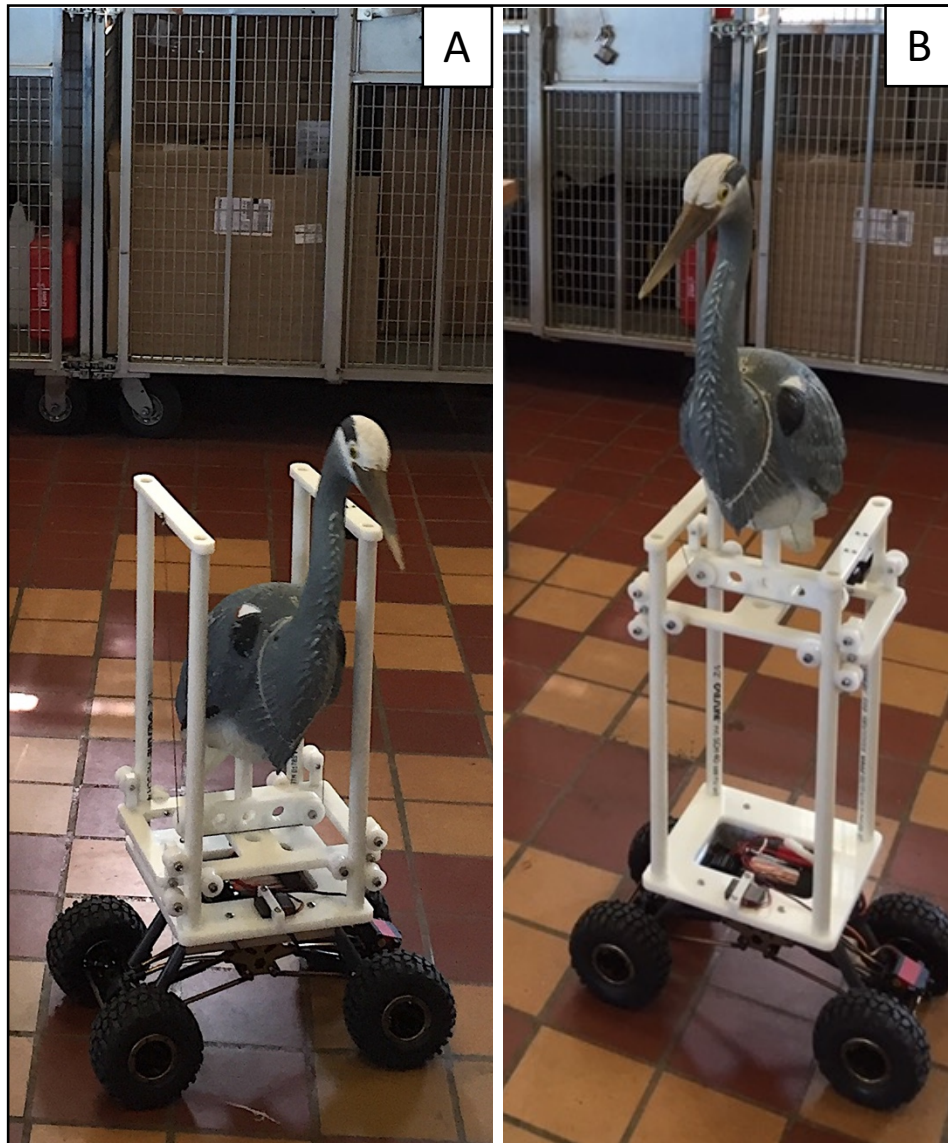
$$\theta = \cos^{-1} \frac{h_3}{|\vec{v}|}$$

where  $\theta$  (theta), is the angle at which the heron is head-tilting,  $h_3$  is the z-coordinate of the heron's head with respect to the base of its neck, and  $\vec{v}$  is the length of the vector created by the heron's neck. The vector created by the heron's neck was first normalized to the orientation of the heron's body via coordinate transfer (procedure in Stewart 2016; also refer to chapter 2).

While there was wide variation ( $SD = 9^\circ$ ), head-tilts were an average of about  $34^\circ$  about the body axis, from vertical, normalized to the heron's body orientation. Therefore, we used about  $34^\circ$  as the angle for the head-tilting treatment. We used the "Angle Meter" iPhone app to set this head-tilt angle for the heron decoy before each head-tilting trial.

We exposed the fish in each of the 4 raceways to 5 head-tilting, 5 control, and 5 upright trials, for a total of 60 trials. Due to scheduling at the hatchery, we were able to conduct the experiments over only 14 days. We used a random sequence generator (via random.org) to pick the orders in which we would run trials with each of the raceways, and each of the treatments.

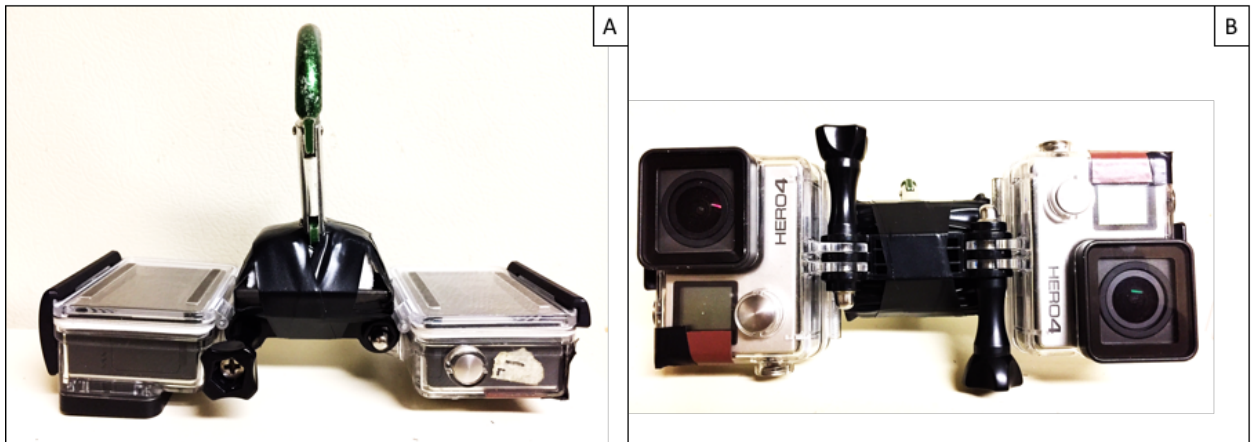
During each experiment, we used the remote controlled crawler to move the decoy to the end of a raceway; this ensured that fish behavior would not be influenced by exposure to the researchers. To standardize the timing and amount of visual exposure of fish to the heron decoy, we kept the elevating platform on which the heron decoy was mounted in the lowest position while using the remote control to wheel it into the appropriate position between trials (Fig. 7a). Once the decoy was in place in front of the correct raceway, the platform was raised via remote control, and the heron decoy (or the control without a decoy) was lifted to the highest position (Fig. 7b), so that the body of the decoy was raised above the height of the ledge of the raceway. Additionally, to limit visual exposure of fish in adjacent raceway to the decoy during trials, blinds were made from styrofoam sheets and placed between raceways. The blind between raceways 2 and 3 to was lengthened, as these raceways were directly adjacent to each other, sharing a wall. Finally, to limit visually exposing the fish to human pedestrian traffic of the hatchery employees, we fashioned cardboard blinds for the sides and ends of the raceways opposite to where we presented the decoy to the fish.



**Fig. 7.** The robotic heron was driven via remote control toward trial raceways, while the lift was in the lowest position (**A**). This was so that the heron decoy was below the sight-line of the fish before trials began. At the start of each trial, the lift was raised to the highest position (**B**).

The robotic heron decoy made a small amount of noise as it was remotely driven in between raceways. However, the ambient noise from the ever running water of 18 flow-through raceways, and the AM/FM radio (which was also always on) were much louder.

Two GoPro HERO4<sup>TM</sup> Silver cameras were hung along the ceiling from a carabiner which was modified with Styrofoam and electrical tape to stabilize a dual camera mount (Figs. 5 and 8). They were suspended from the ceiling of the building on a clothesline mounted on pulleys. Two cameras were used during each trial in case one malfunctioned. Cameras were moved manually over the raceway of interest by climbing a ladder, mounting the camera to the clothesline, and then pulling the clothesline around the clothesline pulley until the camera was in the correct position. Climbing the ladder caused fish to flee. One study found that cleaner fish in coral reefs that were regularly exposed to humans (i.e., divers) needed about  $21 \pm 6.51$  minutes to habituate, and return to cleaning activity after disturbance (Titus et al. 2015). We therefore waited 25 minutes to start trials after shifting cameras. At the end of the wait time, the robotic heron decoy was remotely wheeled into position in front of the appropriate raceway, and trials started immediately when the heron-shaped lawn decoy (or the empty platform) began to raise via remote control.

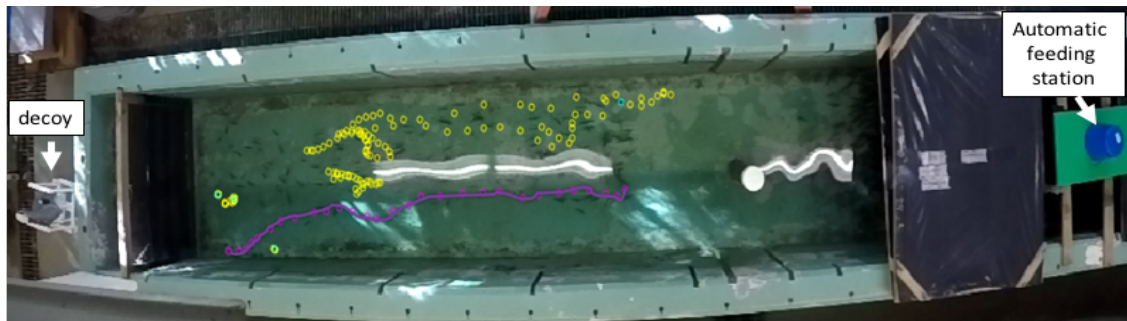


**Fig. 8.** Views of camera mount from the **A.** side, and **B.** front.

After experiments were completed, we used the overhead videos to quantify the responses of a subset of fish within 2m of the heron decoy; we estimated 2m to be a reasonable striking distance of a heron, after taking a large step. We used random.org to generate 10 random coordinates within the first 2 meters of the heron decoy, then chose the 10 nearest fish to those points. In a few instances there were fewer than 10 fish starting the trial within ~2 meters of the robotic heron decoy; in those cases we used all available fish. (See also Statistical Methods, below.) In 6 of our 60 videos, there were no fish within 2m of the decoy; these videos were not analyzed. We used linear marks, at distances of 1.2m and 1.98m to where the heron decoy was presented, that run vertically from the rim to the floor of raceway, on the interior raceway walls, to visually distinguish whether fish within 2 m of the decoy.



We used the software DLTdv5 and DLTdv6 (Hedrick 2008) to digitize the locations of each of the 10 (or fewer) fish in each of the 54 videos. We digitally tracked their locations in every 50th frame (every 5/12 second) for 2,000 frames (i.e., about 16.7 seconds). We used a period of 2,000 frames because this was about how long it took for the heron decoy to raise from its base position to its highest position (Fig. 9). We then used the positional information of the fish to quantify both the speed at which fish swam away from the decoy and the total distance that they had fled. GoPro cameras have fish-eyed lenses, and thus we used an undistort function (written by T. Hedrick, obtained via personal communication) to correct for this problem. Once videos were corrected, we could quantify the speeds at which fish traveled during each 50-frame period, as well as the variance in speeds and distances traveled among individuals within a raceway and among treatments.



**Fig. 9.** Example of a digitized fish trajectory (in purple) during an upright neck treatment. The other circles in the image are locations of other fish during the same 2,000-frame period. The mesh screen on the far left of the raceway was a mechanism by which the hatchery staff kept fish from entering the drainage area. The robotic heron decoy can be seen on the far left.

### *Statistical Methods*

We used the 54 (out of 60) videos that contained fish within the first 2m of the decoy in our analyses. To account for unequal numbers of fish within our 2 m test distance across treatments, as well as a lack of independence among fish within a single raceway (i.e., as schooling animals, individual fish behaviors within a raceway are not independent of one another), we used generalized estimating equations (Liang and Zeger 1986). We used R for all statistics (R Core Team 2013), and the R package “geepack” (Højsgaard et al. 2006) for all generalized estimating equations. We modeled two types of fish responses per trial: ending distances (i.e., distance traveled with respect to starting positions), and maximum speeds (calculated over 50-frame intervals), of all fish over the 2,000-frame period. A priori, we expected that these responses might be affected not only by experimental treatment, but also by group size in the initial cohort of fish within 2 meters of the heron decoy. In addition to group size, we also expected that within-raceway fish responses to the decoy might dampen over time. Therefore, our models included these factors, either directly (as with group size) or by proxy. For example, each raceway was exposed to the heron decoy a little over once per day on average, so we used a time-based autoregressive correlation structure. Our equations were as follows:

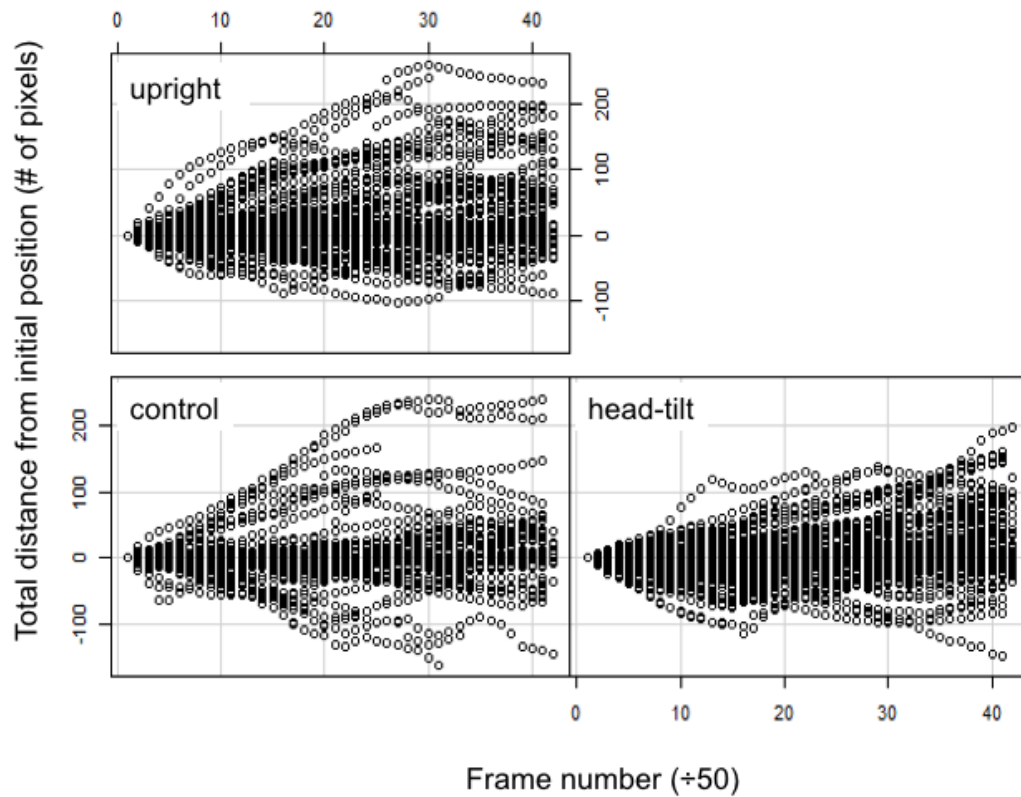
1. Ending Distance of Fish after 2,000 frames = constant + treatment + initial group size, by raceway identity, with an autocorrelation structure related to the number of days passed since the first day of trials

2. Maximum speed (calculated every 50 frames) among fish in 2,000 frames = constant + treatment + initial group size, by raceway identity, with an autocorrelation structure related to the number of days passed since the first day of trials

We then examined p-values via the Wald statistic for all terms within our generalized estimating equations.

### **3.4 Results**

Trajectories of fish as they moved toward or away from the heron decoy relative to their starting position are shown in Fig. 10 (also see Supplemental Fig. S1). Note the visual differences in the shapes of the fish trajectories. Ending distances of fish from the decoy, as compared with the initial fish positions, differed by treatment, and by initial group size (Table 1). Controlling for group size, ending distances in the head-tilting treatment were about 19 pixels farther away from the heron decoy as compared with the control treatment, although this difference was not statistically significant from the control ( $W = 3.43$ ,  $p = 0.064$ ,  $SE = 10.31$  pixels). In the upright treatment, when controlling for initial group size, fish swam about 28 pixels further away from the heron decoy, as compared with control treatment ( $W = 6.68$ ,  $p = 0.0097$ ,  $SE = 10.97$  pixels).



**Fig. 10.** Fish trajectories, in units of distance from their initial position, in response to the control (bottom left), head-tilting decoy (bottom right), and upright heron decoy (top). Positive distances indicate that the fish fled farther away from the heron, and negative distances indicate that the fish swam closer to the heron.

**Table 1.** Output for the generalized estimating equation: Ending Distance of Fish after 2000 frames = constant + treatment + initial group size, by raceway identity, with an autocorrelation structure related to the number of days passed since the first day of trials.

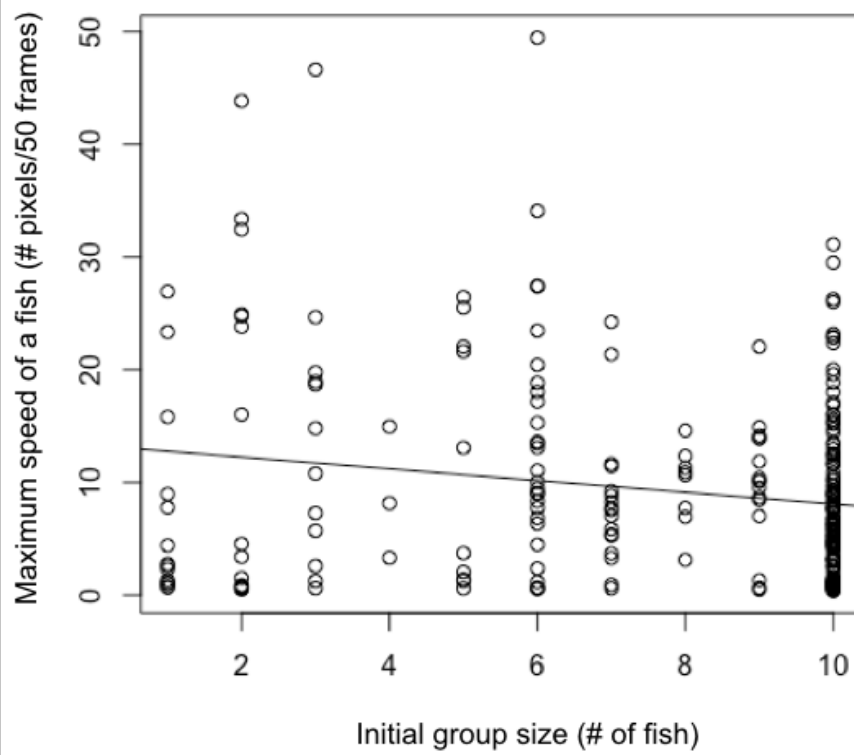
Coefficient	Estimate	Std. Error	Wald statistic	P(> W )
Intercept	31.96	12.04		
Head-tilting	+ 19.09	10.31	3.43	0.064
Upright	+ 28.35	10.97	6.68	0.0097
Initial group size	- 3.39	1.44	5.55	0.019

Fish in larger groups fled less far from the decoy than did fish in smaller groups. For each additional fish in the initial group size, the ending distance decreased by about 3.4 pixels, when controlling for treatment ( $W = 5.55$ ,  $p = 0.02$ ,  $SE = 1.44$  pixels).

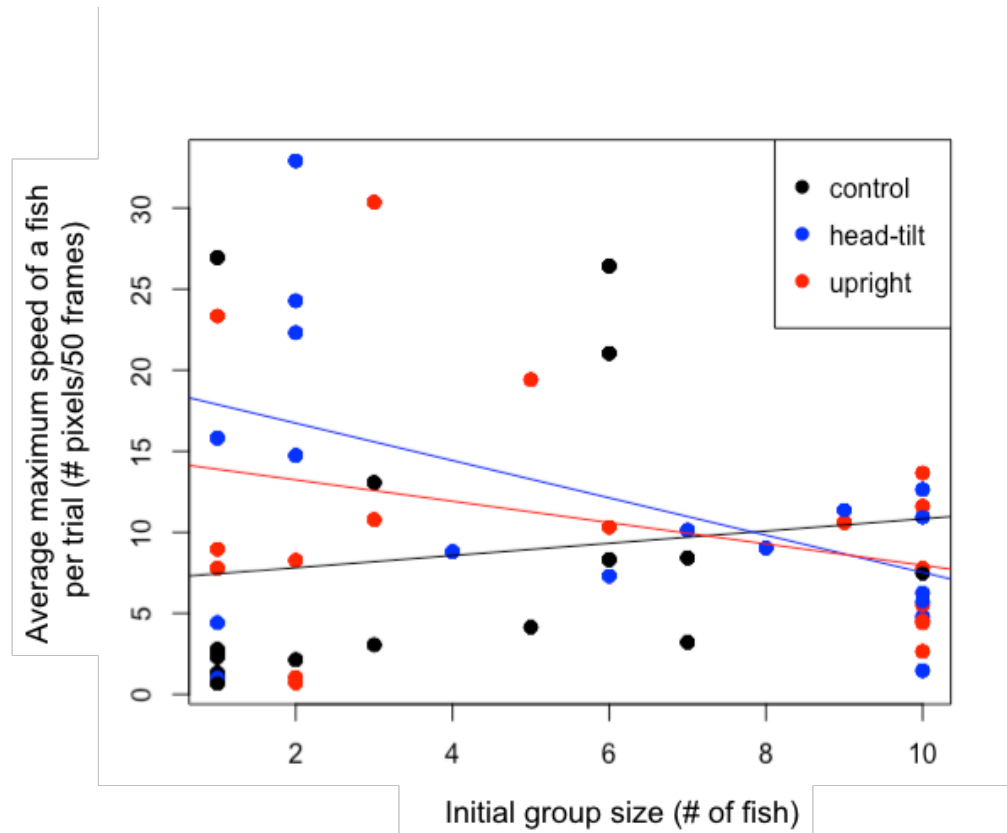
When controlling for initial group size, there was no statistical difference between maximum speeds of fish in head-tilting versus control treatments ( $W = 0.92$ ,  $p = 0.337$ ; Table 2). Nor was there any statistical difference between upright and control treatments ( $W = 0.84$ ,  $p = 0.359$ ; Table 2). However, fish travelled about 0.62 fewer pixels per 50 frames for each additional fish in the initial group within 2m of the heron decoy ( $W = 0.252$ ,  $p = 0.014$ ,  $SE = 0.252$ ; Figs. 12 and 13).

**Table 2.** Output for the following generalized estimating equation: Maximum speed among fish within 2,000 frames = constant + treatment + initial group size, by raceway identity, with an autocorrelation structure related to the number of days passed since the first day of trials

Coefficient	Estimate	Std. Error	Wald statistic	P(> W )
Intercept	12.781	2.085		
Head-tilting	+ 1.661	1.729	0.92	0.337
Upright	+ 1.527	1.667	0.84	0.359
Initial group size	-0.619	0.252	6.05	0.014



**Fig. 12.** When controlling for group size, maximum speeds of fish decrease by 0.619 pixels per 50 frames, for each additional fish in the initial group within 2m of the heron decoy ( $W = 0.252$ ,  $p = 0.014$ ,  $SE = 0.252$ ).



**Fig. 13.** Average maximum speeds of fish generally decreased with increasing initial group size. However, these linear models suggest that those patterns may have been driven by head-tilting ( $t = -4.00$ ,  $p = 0.0001$ ) and upright treatments ( $t = -2.26$ ,  $p = 0.026$ ), and not by the control treatment ( $t = 0.83$ ,  $p = 0.41$ ).

### 3.5 Discussion

Our results suggest that, when controlling from group size, fish swim farther from a heron with an upright neck than from a non-predatory control object, and that the distance they swim from a head-tilting heron is statistically indistinguishable from the distance they swim away from the control object. This is consistent with our prediction that fish would travel farthest from an upright heron, an intermediate distance from a

head-tilting heron, and least far from a control object, and therefore consistent with the idea that herons are evading being detected or recognized by prey by head tilting to make their outlines less recognizable. However, flight distances were statistically indistinguishable between upright and head-tilting treatments. Our results are likely somewhat obscured by lack of control over some elements of the experiment, e.g., initial group size within 2m of the decoy.

Despite our findings with regard to ending distances of fish, we found no evidence that maximum speeds of fish among treatments differ in response to upright-necked herons, head-tilting herons, and a non-predatory control. However, maximum speeds of fish do differ by group size, generally decreasing as group size increases. This is consistent with the idea that individual risk decreases as group size increases. Fish in smaller groups, which are most vulnerable to predation, should swim away more quickly than fish in larger groups, to join other fish, in order to reduce their susceptibility to predation (Hemelrijk and Hildenbrandt 2007; Hemelrijk and Hildenbrandt 2012). We suggest that researchers control for group size in the future, when conducting related experiments.

In this study, we used predator-naïve fish that were bred from wild stock. In Atlantic salmon (*Salmo salar*), hatchery-raised offspring of wild-caught adults had dampened, but not absent, responses to predators (Jackson and Brown 2011). Therefore, we also suggest that any future research related to our work should conduct experimentals with fish that



have been exposed to predators, in order to confirm whether or not our results are biologically meaningful in wild conditions.

Another way to build on our study would be to compare the degree to which herons head-tilt versus the distance between the heron and its prey. If our hypothesis that herons head-tilt to evade detection or recognition continues to be supported, we predict that herons that are closer to their prey should head-tilt more extremely than herons that are farther away from their prey (if prey depth is held constant), in order for the bird to remain at the edge of the prey's Snell's Window. Furthermore, if these predictions were verified, it would help to explain the great amount of variation in heron head-tilt angles.

Like physical traits, behavioral traits are subject to selective forces. For example, an ambush predator should behave in ways that maximizes its ability to successfully hunt, minimizing the possibility of being detected or recognized by prey before it strikes.

Traditional examples of arms races often reference armor-like morphological and chemical defenses, but behavior can be thought of in the context of arms races as well (e.g., Langmore et al. 2003; Kobayashi et al. 2015), co-evolving with various adaptations of other organisms with which they interact.

Head-tilting may be a behavior that co-evolved with a physical adaptation of aquatic prey. Many fish that live near the water surface simultaneously have ventral retinal regions that are specialized for peering into the bright terrestrial world above, and dorsal retinal regions that are specialized for the dim aquatic world below (Pitcher 1993). A few of these fish even have specialized retinal regions that have been hypothesized to allow them to see better around the edge of Snell's Window (Pitcher 1993). If this hypothesis is correct, perhaps this retinal adaptation of the prey has contributed to selection for head-tilting in herons. Perhaps it was the pressure needed in order for the advantages of decreased detectability to outweigh the disadvantage that the prey would be more visually distorted. And perhaps selective pressure is exerted in both directions, with successful strikes after head-tilting selecting for fish with better and better retinal adaptations for viewing the edge of Snell's Window. After all, surface-dwelling fish, and other aquatic organisms that live near the air-water interface are subject to many attacks by aerial and terrestrial predators, including several species of birds, cats, bats, and spiders, as well as a few lizards (e.g., Carl 1987; Altenback 1989; Nyffeler and Pusey 2014; Cutter 2015; HMB personal observation). Even needle fish have been known to attack other fish by leaping out of the water so as to strike at their prey from air to water, and it was hypothesized that they exploit the visual properties of Snell's Window (Day et al. 2016).

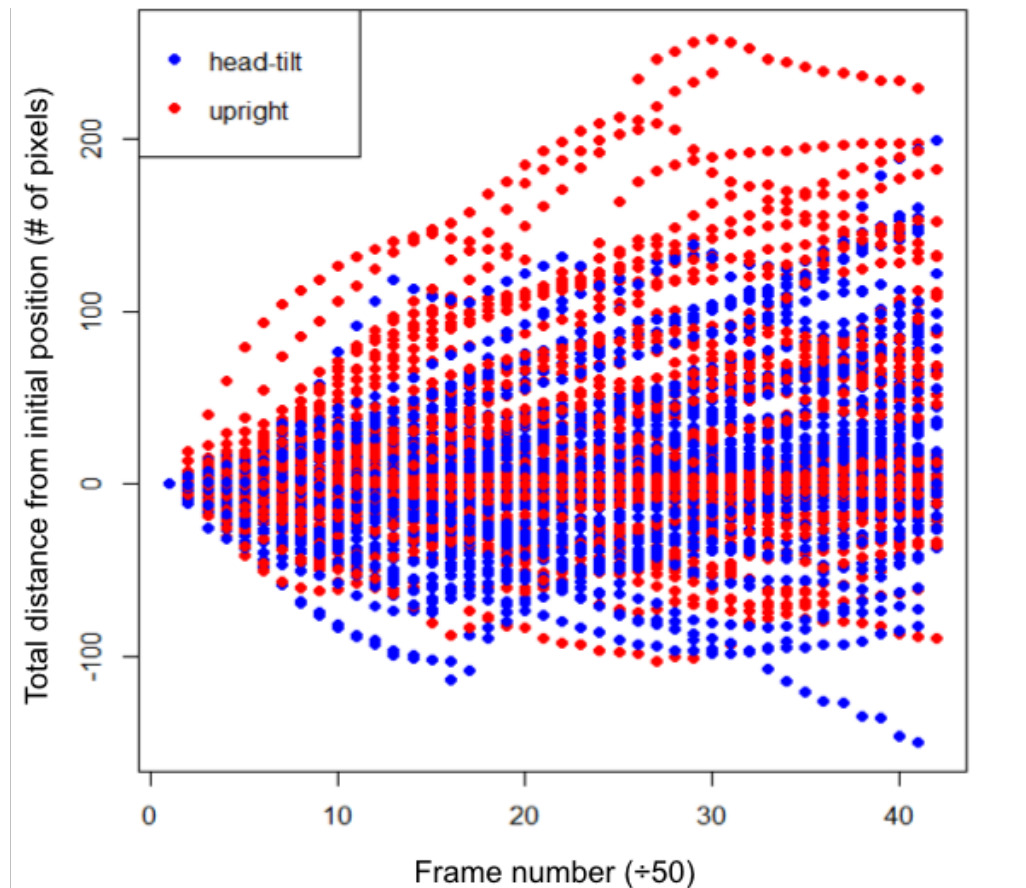
It has also been shown that herons capturing moving prey in the wild struck at more acute angles to the water surface than herons striking at stationary prey in the laboratory (Katzir and Intrator 1987, Lotem et al. 1991). Herons can strike at these acute angles without

head-tilting, by crouching down, and holding their long necks close to their bodies, then striking way out in front of their bodies. Lotem et al. (1991) suggested, and I agree, that this acute strike provides an advantage to the heron by reducing its detectability to prey, due to the visual properties of Snell's Window. Thus, herons may head-tilt for the same exact reason as they strike forward at acute angles to the water surface. There is a remaining question of which circumstances lead to one behavior versus the other. We suggest that it potentially depends on a heron's position in relation to prey position and trajectory at the time point when the heron detects the prey.

Head-tilting in great blue herons was originally hypothesized to be related to sun glint-avoidance (Krebs and Partridge 1973). This hypothesis was generally accepted for over 40 years, and there was other literature that seemed to support the idea that sun glint posed a visual challenge for herons. For example, great blue herons were found to head-tilt more often (Krebs and Partridge 1973) and at greater angles (refer to chapter 2) on sunny than cloudy days. Also, great blue herons were found to have lower foraging success on sunny days versus cloudy days (Bovino and Burt 1979). While these works would seem to support a sun glint-avoidance hypothesis for head-tilting, we know little about how fish behavior might vary on sunny versus cloudy days, relative to the behavior of a heron. Data on this subject would be of interest. Furthermore, my previous work (refer to chapter 2) showed that the amount of sun glint directed toward herons' gazes was not different before versus during a head-tilt, providing strong evidence that head-tilting is not related to sun glint. Perhaps hiding at the edge of Snell's Window is more

advantageous on sunny days when the birds is casting a more distinct shadow. We also tested the hypothesis that a shadow cast by head-tilting could create a refraction-corrected track along which herons could aim and strike at fish (chapter 2). This hypothesis was unequivocally falsified. Therefore, to date, evidence best supports our hypothesis in this study, that herons head-tilt in order to evade being detected or recognized by prey.

### 3.6 Supplemental Material



**Fig. S1.** An overlay of fish trajectories during head-tilt and upright treatments, in units of distance from their initial position. Positive distances indicate that the fish fled farther away from the heron, and negative distances indicate that the fish swam closer to the heron.

### **3.7 Acknowledgements**

We are grateful to CT DEEP, and the supervisors (R. VanNostrand and J. Hays), and other employees at the Burlington Trout Hatchery, for generously allowing us to use their fish and their facilities to conduct our experiments. We thank J. Hays, in particular, for installing a clothesline on their ceiling for our overhead cameras. M. Drobney and P. Glaude were instrumental in designing and building the robotic heron decoy. M. Watkins and K. Cooper digitized fish movements and helped to organize data sheets. T. Hedrick taught HMB how to use DLTdv5 to digitize animal behaviors. We also thank the Link Foundation and Smithsonian Institution for a research fellowship that allowed HMB to record free-living, foraging herons, which made it possible for us to quantify head-tilt angles, as well as HMB's Smithsonian-affiliated advisor during that time period, C.S. McKeon. Finally, we thank E. Schultz, H. Dierssen, A. Moiseff, E. Adams, and all reviewers for helpful commentary.

### **3.8 Animal Care Statement**

These experiments were performed at the Burlington Trout Hatchery, under University of Connecticut IACUC exemption (E15-010), and with oversight by the Connecticut State Department of Energy and Environmental Protection. The University of Connecticut IACUC also approved a reciprocity agreement (# R14-010) with the Smithsonian ACUC (# 2014-12) for oversight of behavior observations of free-living herons that allowed us to quantify naturally occurring head-strike angles. The work with free-living herons, and

baitfish, which allowed us to quantify head-tilt and strike angles was performed under a permit through the Florida Wildlife Commission (Permit # LSSC-14-00061).

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