The light's in my eyes: optical modeling demonstrates wind is more important than sea surface-reflected sunlight for foraging herons

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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. Intense sun glint is common at the air-water interface, and it obscures visual cues from submerged prey. Visually-hunting, cross-media predators must therefore solve the problem of glint to hunt effectively. One obvious solution is to turn away from the sun, which would result in reduction of glint effects. However, turning too far will cast shadows over prey, causing them to flee. Therefore, we hypothesized that foraging herons would orient away from, but not directly opposite to the sun. 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. To test our hypothesis, 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 and therefore they must have some other, not yet understood, means of compensation, either anatomical or behavioral. Instead of facing away from the sun, herons tended to adjust their position to face into the wind at higher wind speeds. We suggest that radiative transfer modeling is a promising tool for elucidating the ecology and evolution of air-to-water foraging systems.

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19 **Abstract**

20   Multiple lineages of birds have independently evolved foraging strategies that involve catching

21   aquatic prey by striking at them through the water's surface. Diurnal, visual predators that hunt

22   across the air-water interface encounter several visual challenges, including sun glint, or

23   reflection of sunlight by the water surface. Intense sun glint is common at the air-water interface,

24   and it obscures visual cues from submerged prey. Visually-hunting, cross-media predators must

25   therefore solve the problem of glint to hunt effectively. One obvious solution is to turn away

26   from the sun, which would result in reduction of glint effects. However, turning too far will cast

27   shadows over prey, causing them to flee. Therefore, we hypothesized that foraging herons would

28   orient away from, but not directly opposite to the sun. Our ability to understand how predators

29   achieve a solution to glint is limited by our ability to quantify the amount of glint that free-living

30   predators are actually exposed to under different light conditions. Herons (*Ardea* spp.) are a

31   good model system for answering questions about cross-media hunting because they are

32   conspicuous, widely distributed, and forage throughout a variety of aquatic habitats, on a variety

33   of submerged prey. To test our hypothesis, we employed radiative transfer modeling of water

34   surface reflectance, drawn from optical oceanography, in a novel context to estimate the visual

35   exposure to glint of free-living, actively foraging herons. We found evidence that *Ardea* spp. do

36   not use body orientation to compensate for sun glint while foraging and therefore they must have

37   some other, not yet understood, means of compensation, either anatomical or behavioral. Instead

38   of facing away from the sun, herons tended to adjust their position to face into the wind at higher

39   wind speeds. We suggest that radiative transfer modeling is a promising tool for elucidating the

40   ecology and evolution of air-to-water foraging systems.

41

42   **Introduction**

43   Birds have repeatedly, and independently, evolved foraging strategies that involve detecting prey

44   in water, and striking at them through the air-water interface. To do so successfully, they must

45   contend with a number of visual challenges imposed by the optical properties of the water itself.

46   First, water surfaces can reflect light. Sun glint (hereafter, "glint") refers to the reflection of

47   sunlight by a water surface, directly toward the viewer (Hochberg et al., 2011; Preisendorfer &

48   Mobley 1986). Glint obscures detection of upwelling light from beneath the surface of the water,

49   making it more difficult to see objects below the surface. Humans experience glint as visible

50   bright spots on the surface of the water. Glare is the visual discomfort from the direct reflection

51   of the sun light into their eyes (e.g., Signoroni et al., 2020).

52

53   Cross-media predators, by definition, are attempting to locate submerged prey, and therefore we

54   expect them to have evolved ways to compensate for the effect of glint. One obvious method of

55   reducing the effect of glint is to turn away: an animal that forages at the air-water interface

56   should orient itself generally away from the sun under clear sky conditions if it aims to reduce

57   visual exposure to glint. But by how much? The amount of glint exposure is a complex function

58   of the viewing direction, field of view of the detector or eye, topography of a wind-blown sea

59   surface, sun elevation and the spectral distribution of light.

60

61   Radiative transfer modeling, used in optical oceanography, has shown that glint is generally

62   reduced with an increasing difference in bearing from the sun (Mobley, 1999). For example,

63   assuming 5 m/s wind, a sun elevation of 60°, and a viewing angle looking 40° downward with

64   respect to the horizon, the sea surface would reflect only about 3% of the skylight incident upon

65   the sea surface for an animal viewing the sea surface facing directly opposite (180°) to the sun's

66   bearing. This percentage remains fairly similar until the viewer is facing perpendicular (90°) to

67   the sun's bearing, but begins to rise fairly quickly thereafter, to about 12% when facing directly

68   into the sun's bearing (Fig. 7 in Mobley, 1999). Under higher wind conditions and/or when the

69   sun is directly overhead (sun elevation 90°), orientation plays less of a role in reducing glint

70   (Zhang et al. 2017).

71

72   However, aquatic birds that hunt during the daytime must compensate for an additional

73   challenge: they must be within striking distance of their prey without causing prey to flee. Even

74   though glint is lowest at 180° to the sun's bearing, this is also the bearing that would cause a

75   predator to hunt directly into its own shadow. Several aquatic prey species are known to flee

76   when shadows pass overhead (e.g., Forward, 1977; Roberts, 1978; Yoshizawa & Jeffery 2008).

77   Therefore, a bird hunting across the air-water interface on a sunny day is likely trading off its

78   ability to see prey against the prey's ability to see them.

79

80   Mobley (1999) used radiative transfer modeling to show that when orienting a light detector at

81   about 135° away from the bearing of the sun while measuring remote sensing reflectance of

82   oceanic environments, the view of glint from the water surface is as low as possible over a wide

83   range of water surface and environmental conditions, without facing directly into self-shadow.

84   When the sun is overhead, however, orientation does not play a role in reducing glint. Mobley's

85   work, by extension, suggests that although there is a range of orientations at which birds could

86   reduce their exposure to glint, orienting at 135° to the bearing of the sun is the position in which

87   birds hunting across the air-water interface can best trade off reducing glint exposure, while also

88   avoiding casting shadows over potential prey. This logic assumes that birds see and perceive

89   glint as we do, an assumption that may not be justified, given the limitations on what we know

90   about avian vision. Nonetheless, there is some limited, and anecdotal evidence that they do and

91   that they may be trading off glint exposure against their own detectability as we predicted based

92   on Mobley's (1999) radiative transfer modeling. For example, Brown Pelicans (*Pelecanus*

93   *occidentalis*), were found to orient at an average of 135.6° to sun bearing (s.d. = 36.1°) as they

94   dove for fish (Carl, 1987). We have also documented that a tern diving for fish in a pond, did so

95   at about 140° to sun bearing, (documented on video three times in a row; it also did so several

96   times in a row before the lead author started recording the behavior; Supplemental Video 1).

97   Even the behavior of non-aquatic avian predators suggests that they experience challenges from

98   intense light conditions as we do. When the dark facial masks on Masked Shrikes (*Lanius*

99   *nubicus*) were painted white, they oriented away from the sun to a greater degree than shrikes

100   with black masks (Yosef, Zduniak & Tryjanowski, 2012.), suggesting that sunlight reflecting

101   from their facial feathers caused some visual discomfort.

102

103   Visual ecologists have demonstrated that orientation is important in visual function (e.g.,

104   Muheim, Phillips & Åkeesson, 2006; Penacchio et al., 2015), but there are only a handful of

105   studies that investigate orientation specifically with regard to hunting strategies (Carl, 1987;

106   King & LeBlanc, 1995; Yosef, Zduniak & Tryjanowski, 2012. ; Huveneers et al., 2015).

107   Orientation with respect to the sun may affect the ability to see prey, and therefore should be

108   explicitly considered when studying the foraging ecology of visual, cross-media predators. Here,

109   we examine the hypothesis that avian cross-media predators use body orientation to reduce glint

110 in their strike zones while hunting, and that they do so in a manner that trades off glint exposure

111 against self-shadow into their strike zones (Fig. 1). To test this hypothesis, we studied diurnal

112 herons of the genus *Ardea*, which belong to a clade of piscivorous birds that have been

113 specializing to hunt across the highly reflective air-water interface for over 50 million years

114 (Prum et al., 2015).

115

116 We studied, specifically, two daytime-active herons, Great Blue Herons (*Ardea herodias*) and

117 Great Egrets (*Ardea alba*; hereafter, "herons"). These species are good models for answering

118 questions about cross-media hunting because they are numerous, conspicuous, widely

119 distributed, and forage throughout a variety of aquatic habitats, on a variety of submerged prey.

120 If herons were using orientation to trade off glint and self-shadow, we predicted that they would:

121 a. orient in ways that minimize glint, and maximize the signal from upwelling light (i.e., the light

122 reflected by potential submerged prey items), as compared with what would be expected if heron

123 orientation were random, and b. specifically, we expect them to orient at an average of 135° to

124 the sun bearing. Great Blue Herons tend to be slightly more crepuscular than the more diurnal

125 Great Egrets (McNeil, Benoît & DesGranges, 1993). In gathering data from both, our intent was

126 to obtain generalizable information about how herons might compensate for glare while hunting

127 through the air-water interface, over a wide range of daylight conditions. We employed radiative

128 transfer modeling in a novel context to directly estimate the actual exposure of individual birds

129 to glint, on the basis of their orientation to the sun, the sun elevation, and light conditions.

130

131   We also considered the hypothesis that heron body orientation could be related to wind.

132   Orientation with respect to both sun position and wind direction have been widely recognized as

133   important physiological mechanisms by which animals regulate body and microhabitat

134   temperatures (e.g., Orr, 1970; Walsberg, 1993; Fortin Larochelle & Gauthier, 2000; and many

135   others). If herons were orienting to prevent loss of body heat, we predicted that heron orientation

136   would correlate with wind direction, particularly at higher wind speeds. In addition, because of

137   light reflecting from differently oriented wave facets, the advantages of orienting away from the

138   sun are also reduced under higher wind speeds compared to flat conditions. Hence, we predicted

139   that they would be more likely to face into the wind, regardless of sun position, as wind speed

140   increased.

141

142   **Materials & Methods**

143   In June 2013, January 2014, and January-February 2015, we opportunistically obtained 279

144   observations of 68 free-living, foraging herons in southern Florida (Fig. 2). As our study

145   involved focal animals in the field, it was not possible to record data blind. In areas where an

146   individual heron seemed to be actively guarding a foraging area (e.g., by chasing other

147   individuals away), we sampled the site only once. However, in areas where there were several

148   herons foraging, we were able to obtain observations of different individuals at the same

149   location. From a minimum distance of 20m, using binoculars (Nikon Monarch 3, 10x42), we

150   observed individual foraging herons, and recorded up to 6 instantaneous samples of their body

151   and head orientations, or fewer, if the individual flew away. In 2013, instantaneous samples were

152   spaced 5 minutes apart, while in 2014 and 2015 samples were taken every two minutes. At the

153   beginning of each observation, we noted the date, time, and the species. We noted sun visibility

154   and cloud cover, as our predictions depended on the sun's being visible. We also noted wind

155   bearing and speed category: calm/virtually undetectable (approximately 0 m/s); leaves rustle

156   (approximately 5 m/s); branches sway (approximately 10 m/s); trees sway (approximately 15

157   m/s). If the wind speed and direction were noticeably variable, we updated this information

158   during every instantaneous sample. We also noted whether the bird's shadow was obstructed

159   (e.g., by emergent vegetation) during every instantaneous sample. The orientation of the birds'

160   bodies and heads, and the orientation of the wind were estimated in the field with a handheld

161   compass. Exact sun bearing and elevation were later retrieved from the National Oceanographic

162   and Atmospheric Administration's online sun position calculator, based on the time recorded for

163   each instantaneous sample in each observation. Also, the approximate latitude and longitude of

164   each location were obtained from Google Earth. We were then able to calculate the estimated

165   orientation differences between the birds and the sun, and between the birds and the wind, to use

166   in analyses. After the final field season, we quantified error associated with estimating heron

167   orientation. To do so, a field assistant placed a Great Blue Heron lawn ornament in 24 different

168   directions and recorded its real orientation while the lead author (who made all compass

169   measurements in the field) estimated each orientation from a distance of 20m, with the same

170   binoculars that were used in the field (Nikon Monarch 3, 10x42). Our estimations of body

171   orientations of a Great Blue Heron lawn ornament were within an average of 9.3° (s.d. = 7.5°, N

172   = 24). Therefore, we believe our estimates of heron body orientation are sufficiently accurate to

173   test the hypotheses of interest in this study.

174

175   Using the *Hydrolight*® radiative transfer model (Mobley, 1998), we estimated absolute and

176   relative glint in the green spectrum (550 nm). We defined relative green glint as green glint

177   divided by the all incoming green light in the field of view (i.e., water-leaving radiance plus

178   radiance reflected by the sea surface). The relative measure is a type of signal-to-noise

179   measurement. We used green light exclusively, because we wanted our estimates of glint to be

180   conservative, in that they would maximize background brightness and minimize relative glint. In

181   general, green light penetrates furthest into coastal waters (Kirk, 2011), and is therefore the light

182   most available to be reflected by the seafloor, and exit the water as upwelling light. Therefore, in

183   comparison, the contribution of glint is lower relative to the upwelling light in the green

184   spectrum versus in other spectral regions.

185

186   We also used conservative but realistic values representing conditions in Florida, and conditions

187   for wild foraging herons, for all variables in *Hydrolight*®, to obtain conservative estimates for

188   glint. We modeled reflectance for a light-colored sand (ooid), which is both typical of many

189   Florida coasts, but also creates high reflectance off of the sea floor, thus increasing the relative

190   signal of upwelling light as compared with glint. We used a medium value for light attenuation

191   in the water by indicating that light would attenuate by half for every meter below the sea surface

192   (McPherson et al., 2011). We also used a water depth of 28 cm based on multiple records of the

193   water depths in which herons forage in Florida (Powell, 1987; Bancroft, Gawlik & Rutchey,

194   2002). We ran the model under two wind conditions: 5 m/s, and 10 m/s. We also ran each of

195   those models under two light conditions: where the sun was visible, and where it was obstructed

196   by clouds.

197

198 To continue in our effort to gain conservative absolute and relative estimates of green glint, we

199 also only retrieved outputs from a viewing direction of 40° to the nadir, because this viewing

200 direction minimizes the proportion of skylight reflected at the sea surface under multiple wind

201 speed scenarios (see Fig. 6 in Mobley, 1999).

202

203 We generated interpolated heat maps of absolute and relative glint in MATLAB (2015), using

204 estimates based on sun elevations of 0°, 15°, 30°, 45°, 60°, 75° and 90° from the horizon.

205 Finally, we used two-sample t-tests to compare estimates of visual exposure to glint for each

206 heron body orientation with estimates of glint exposure that we would expect if heron orientation

207 were random, using coordinates generated from random.org, to test the prediction that herons

208 would orient in a manner that reduced visual exposure to glint.

209

210 All other statistical analyses were performed in R (R Core Team, 2013). To examine heron

211 orientation relative to sun position, we used only instantaneous samples where herons' heads

212 were oriented in the same direction as their bodies, and where the herons' shadows were cast

213 over water (i.e., unobstructed by emergent vegetation, and not cast onto land), and the sun was at

214 least partially visible. To test the prediction that herons would orient 135° to the bearing of the

215 sun, we regressed the absolute difference between sun bearing and heron bearing (i.e. heron

216 orientation relative to sun bearing), against sun elevation, using generalized estimating equations

217 (Liang & Zeger, 1986) with the "geepack" package in R (Højsgaard, Halekoh & Yan, 2006). We

218 used sun elevation as the independent variable instead of time, so that we were comparing heron

219 orientations under consistent sun positions each day. To account for use of multiple observations

220   for some individual herons, which are likely correlated, we used generalized estimating

221   equations (GEE). GEE, an extension of generalized linear models, is a statistical approach for

222   estimating regression parameters with clustered data (Liang & Zeger, 1986). We used

223   "individuals" as grouping factors in our GEE model. We also used unstructured correlation

224   matrices because we were unsure of what, if any, kind of relationship there might be among

225   intra-individual data points. We then used the Wald-statistic to test the overall significance of the

226   regression. As there is no package to estimate power or effect size based on a Wald test, at

227   present, we estimated the effect size of our findings using a power analysis based on a

228   generalized least squares linear model of our data using the "pwr" package (Champely, 2015).

229   We similarly regressed the absolute value of the difference between wind and heron orientation

230   versus wind speed category; and the absolute value of the difference between sun and heron

231   orientation versus wind speed category as an ordered factor.

232

233   **Results**

234   Our prediction that herons would orient in a manner that suggested trading off reducing glint and

235   self-shadow in their strike zones was not supported. We detected no departures from random

236   orientation with respect to sun bearing in herons, across all sun elevations ($y = 89.37° - 0.02x$;

237   $W = 0.003$; $p = 0.96$). This held true no matter whether we included the whole data set in the

238   analysis, or just the subset of the data from when both the sun and the heron's shadows were

239   visible (Fig. 3a-b). The calculated effect size when regressing heron orientation relative to sun

240   bearing versus sun elevation was miniscule ($[r^2 / (1 - r^2)] = {\sim}0.0002$).

241

242   Overlaying our orientation data onto our heat maps displaying absolute and relative estimates of

243   green glint added further evidence that herons are not using body orientation to reduce visual

244   exposure to glint (Fig. 4). We decided to use only the heat maps we generated for 5 m/s wind

245   speed for analyses because the heat maps generated for 10 m/s wind appeared nearly identical.

246   There was no difference between the glint estimated at each heron orientation to the sun and glint

247   that would be experienced at random, either in absolute (t = 1.76, p = 0.08) or relative estimates

248   of green glint (t = 1.55, p = 0.12) with a visible sun. With a completely obstructed sun, glint was

249   still no different from random for absolute (t = 0.14, p = 0.89), or relative estimates of green glint

250   (t = 1.10, p = 0.27).

251

252   In support of our last hypothesis, herons tended to face more into the wind with increasing wind

253   speed. With each increase in ordered categorical wind speed, herons faced about 31.70° (SE =

254   9.39°) further toward the sun (W = 114, p = 0.0007) (Fig. 5).

255

256   **Discussion**

257   Our data provide strong evidence that herons are not using body orientation with respect to sun

258   position as a behavioral mechanism for reducing glint in their strike zone. Herons, when foraging

259   through the highly reflective air-water interface, are not avoiding orienting in directions with the

260   highest estimated exposure to glint, whether in absolute terms, or relative to incoming light, and

261   they are not trading off glint and shadow in their strike zones.

262

263 Our data also showed that as wind speed increased, herons tended to face more head-on into the

264 wind. In retrospect, this is not surprising. One likely explanation for orienting to the wind is that

265 herons are orienting for thermoregulatory purposes. Facing into the wind has been shown to

266 decrease heat loss in birds (e.g., Fortin Larochelle & Gauthier, 2000).

267

268 Herons, and other cross-media hunters, may compensate for glint in other ways. Krebs &

269 Partridge (1973) hypothesized that Great Blue Herons tilt their heads and long necks toward the

270 sun – in a foraging behavior known as "head-tilting" (Meyerriecks 1962) – to effectively shift a

271 perceived area of glare out of their intended strike path. However, their idea was not fully tested,

272 and further research is required to assess whether herons are head-tilting to compensate for glint

273 effects, or has a different function. Relatedly, differences in head placement during foraging

274 might account for some variability in heron body orientation with respect to sun elevation.

275 Future research could investigate the direction of viewing, and eye movement in relationship to

276 glint.

277

278 Because light that is reflected from water surfaces is polarized, some form of polarization vision

279 could be useful to cross-media hunters. Theoretically, there are at least two ways to filter

280 polarized light: before the image is projected onto the retina, or after. For polarized light to be

281 filtered prior to reaching the retina, herons would need an anatomical feature capable of

282 excluding it (as polarized sunglasses would). However, we are unaware of any evidence for such

283 anatomical features in any natural visual systems. For polarized light to be filtered after reaching

284 the retina, we would suggest some neurological capability that allows herons to detect, and

285   subsequently ignore the polarized light as "noise", similar to how we would filter out a din of

286   many voices while conversing with a friend in a crowded restaurant. This possibility seems much

287   more likely. There is considerable evidence that animals across many taxa can see patterns of

288   light polarization, including some behavioral evidence in birds (reviewed in Muheim, 2011). We

289   suggest that behavioral studies designed to detect whether avian cross-media predators exhibit

290   polarized light sensitivity would be fruitful for understanding the ability of these birds to hunt

291   successfully in the face of intense glint.

292

293   Herons may be a good system in which to look for a mechanism for polarization vision in birds

294   because they do not seem to be behaviorally compensating for glint. To date, we only have some

295   very basic details about herons' visual anatomy. In Great Blue Herons, fine structures of the

296   pecten (Braekevelt, 1991), rods and cones (Braekevelt, 1994) and cone pigments (Braekevelt &

297   Young, 1994) have been studied. Their rod to cone ratio is also documented; it is 0.6:1, which

298   puts them in between the diurnal herons (e.g., the Tricolored Heron, *Egretta tricolor*, has a rod to

299   cone ratio of 0.3:1) and the nocturnal herons (e.g., the Yellow-crowned Night Herons,

300   *Nycticorax violaceus*, has a 2.3:1 rod to cone ratio; Rojas et al., 1999). Generally, higher rod to

301   cone ratios produce better night vision than lower rod to con ratios (Rojas et al., 1999). In Great

302   Egrets the only scholarly reference we found regarding their eye anatomy dates back to a 1917

303   book, in which the basic macrostructure of the pecten, and the "dominant color" of the fundus

304   were described (Wood, 1917).

305

306   Although we have suggested some avenues of study to investigate other potential behavioral or

307   anatomical mechanisms for reducing glint exposure in herons, it is possible that there are cross-

308   media predators that do use body orientation to mitigate effects of glint. There is some anecdotal

309   evidence for this behavior in Brown Pelicans (*Pelecanus occidentalis*) and terns (Carl, 1987;

310   Supporting Information). Therefore, we suggest further study of body orientation relative to sun

311   bearing in these, and other, plunge-diving birds.

312

313   Lastly, we suggest continuing to use radiative transfer modeling to better understand the light

314   conditions that air-to-water cross-media predators face while foraging. This new tool might also

315   be useful for re-examining work from previous studies, for example on the physical conditions

316   that affect foraging success in piscivorous birds (e.g., Grubb, 1977; Bovino & Burtt, 1979; Carl,

317   1987). Understanding the conditions under which birds view their prey will lead to deeper

318   understanding of their visual and behavioral ecology.

319

320   **Conclusions**

321   In this study, we tested the hypothesis that foraging herons would orient away from the sun to

322   avoid experiencing glare due to sunlight reflecting from surfaces of the water bodies in which

323   they hunt. Field observations of heron body orientation, along with our estimations of sun glint

324   via radiative transfer modeling provided evidence against our hypothesis; herons did not tend to

325   orient in a manner that reduced their exposure to glint, but rather oriented to face the wind at

326   higher wind speeds. Radiative transfer modeling, a tool from optical oceanography, was useful

327   for investigating visual and behavioral ecology in this air-to-water foraging system, and should

328   be considered in similar studies.

329

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335

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424

Figure 1

Schematic representation of an 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.
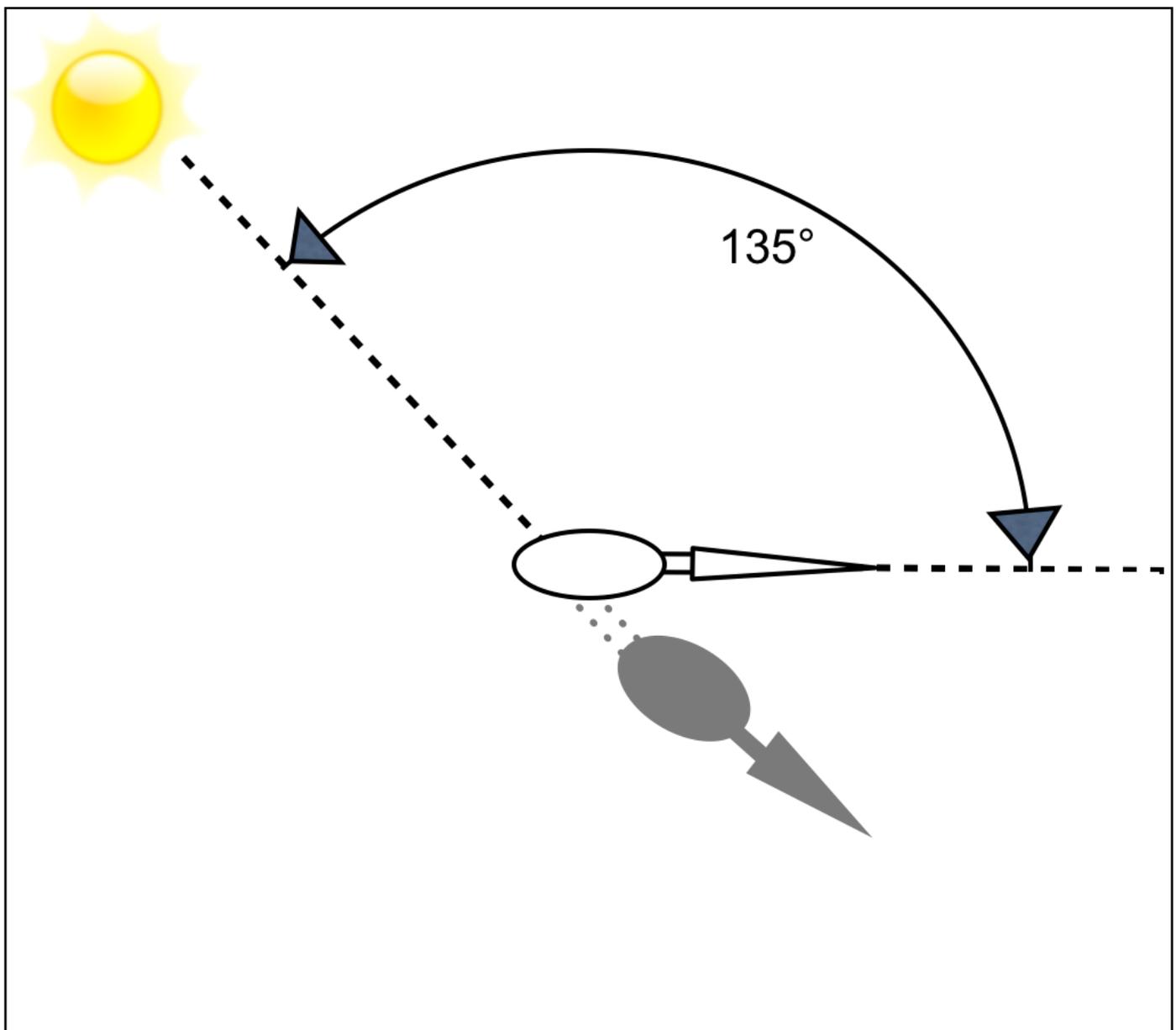
Figure 2

Locations at which herons were observed in southern Florida, USA.

Circles indicate where data were collected. Some circles overlap more than one sampling location. Image Credit: The map was cropped from the original, "Administrative Map of Florida," created by Eric Gaba, via Wikimedia Commons (c) 2008 (user ID: Sting, CC BY 3.0).
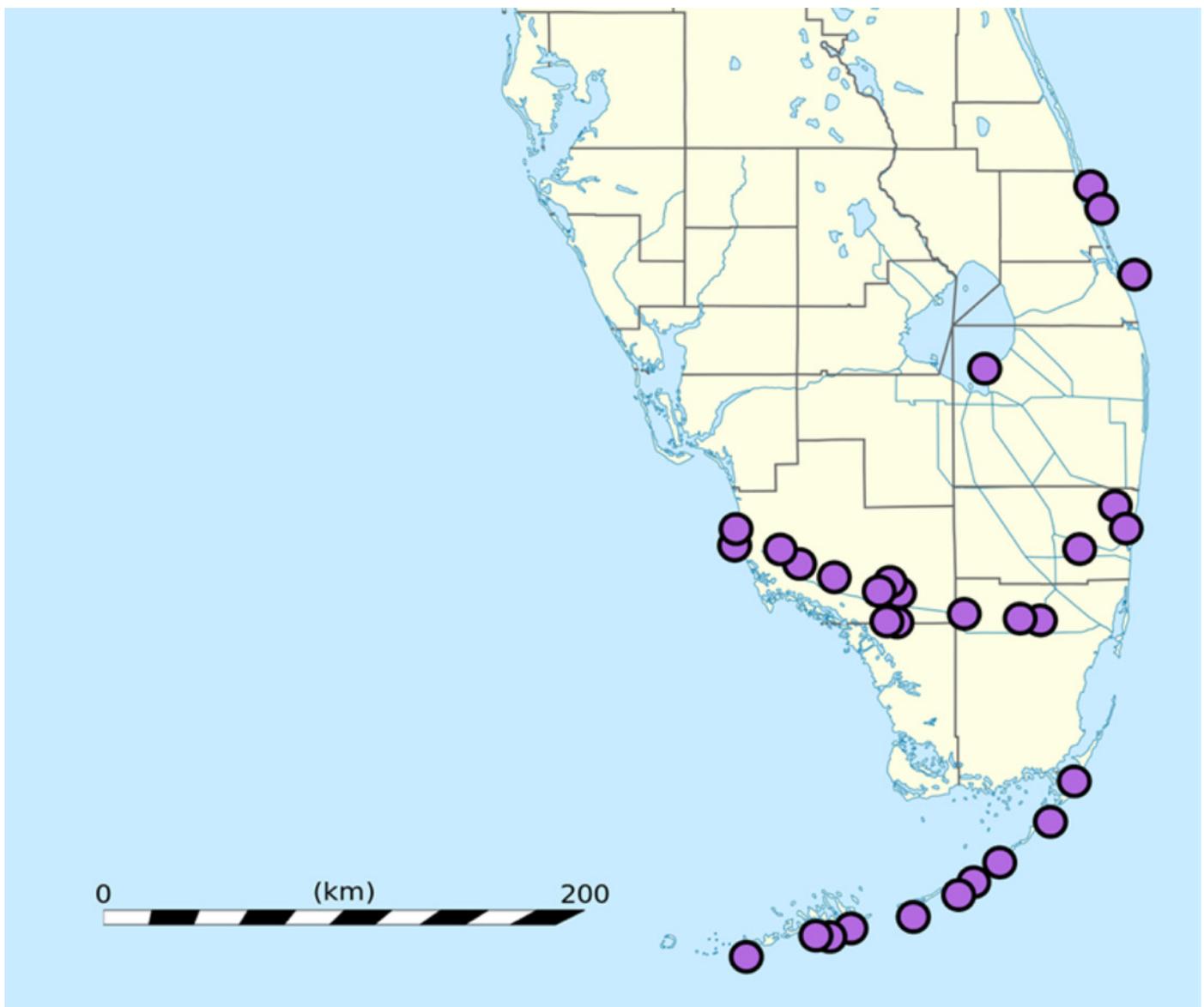
Figure 3

Scatterplots of our data, using points where heron's head and body orientations were in parallel.

In both graphs, 0° on the x-axis indicates that the sun is on the horizon, and 90° indicates that the sun is overhead. On the y-axis, 0° indicates that the heron was facing directly into the sun, and 180° 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 ($p = 0.96$).
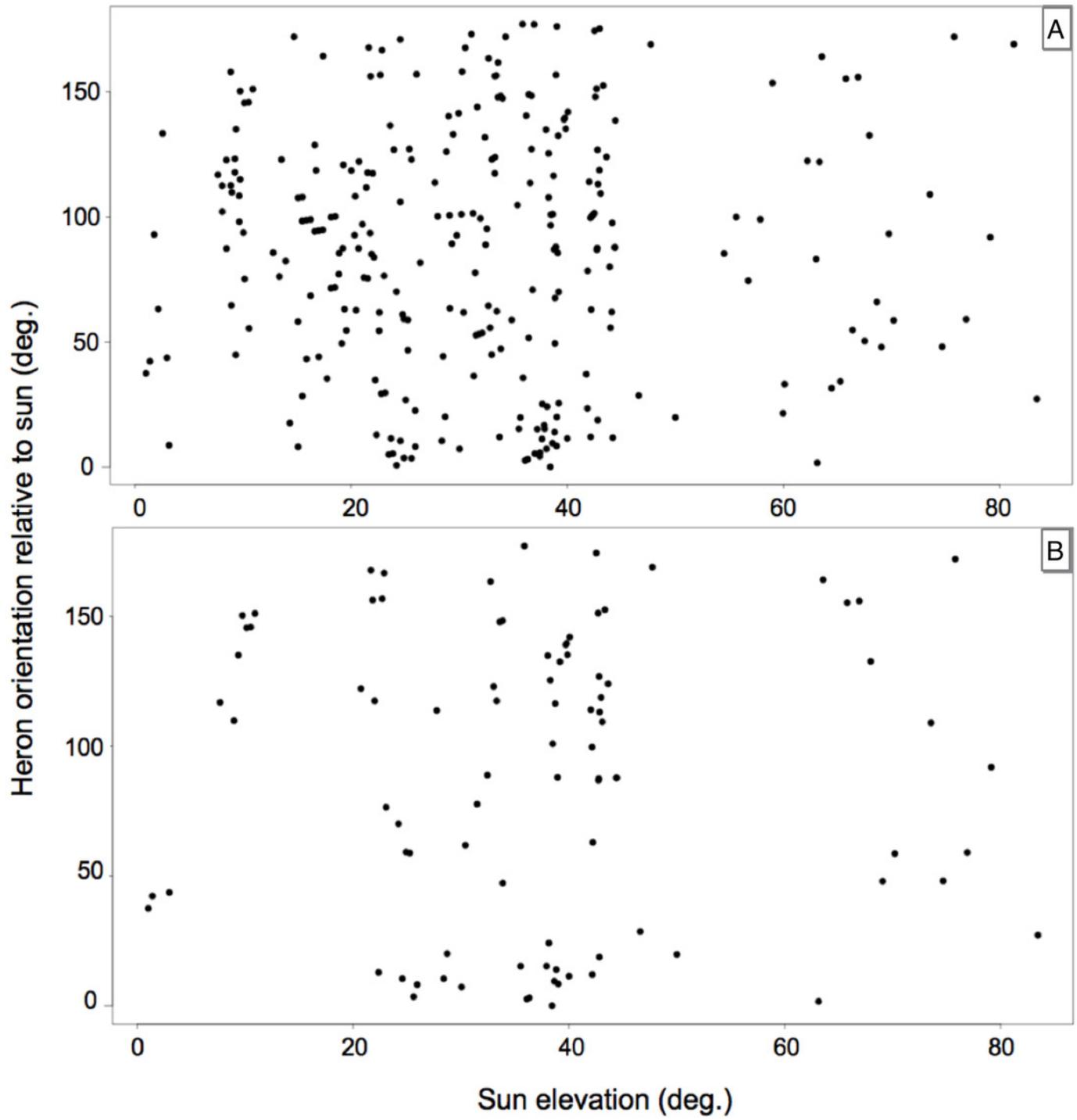
Figure 4

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.

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. (Heat maps for wind speeds of 10 m/s were nearly identical, and are not shown here.)
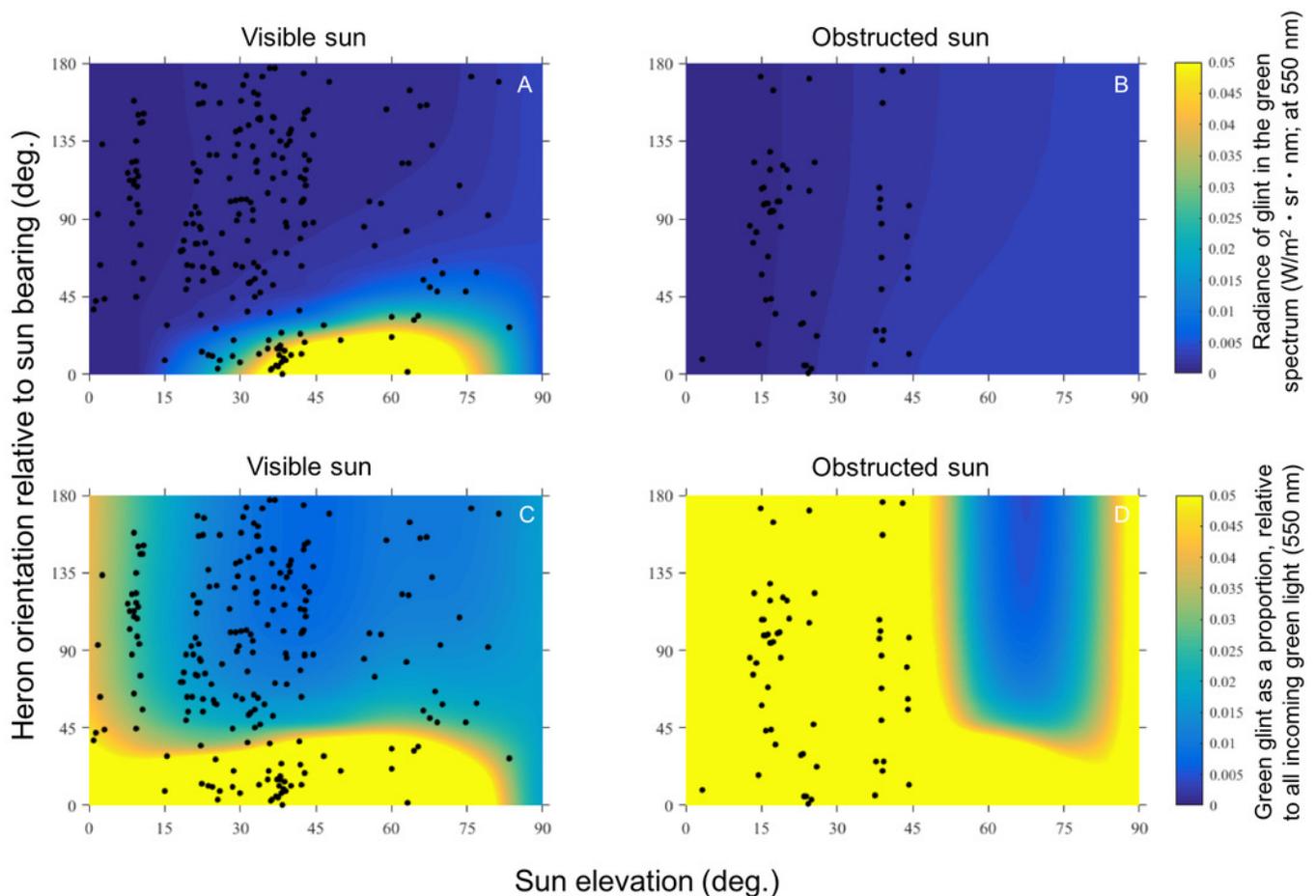
Figure 5

Box plot of heron orientation with respect to the bearing of the wind by wind speed category (0 = calm or ~0 m/s; 1 = leaves rustle or ~5 m/s; 2 = branches sway or ~ 10 m/s; 3 = trees sway or ~15 m/s).

On the y-axis, 0° indicates that the heron was facing directly into the wind, and 180° indicates that it was facing opposite to the wind. With each increase in ordered categorical wind speed, herons faced about 31.70° (SE = 9.39°) further toward the sun (W = 114, p = 0.0007).