



Seafinding revisited: how hatchling marine turtles respond to natural lighting at a nesting beach

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Abstract

Hatchling marine turtles emerge at night from underground nests on oceanic beaches and then use visual cues to crawl from the nest site to the sea (“seafinding”). However, the light wavelengths (λ 's) used to accomplish this orientation have not been thoroughly documented, nor do we understand why some λ 's are favored over others. We measured nocturnal radiance on the horizon at 20 nm intervals between 340 and 600 nm at two nesting beach sites and then, under laboratory conditions, determined the lowest intensities of those λ 's that induced green turtle and loggerhead hatchlings to crawl toward each light source (a low positive “phototaxis threshold”). Both species were similarly sensitive and were attracted to all λ 's. Radiance measures at all λ 's were greater toward the seaward horizon than toward the landward horizon, providing an important orientation cue regardless of variation in lunar illumination. Previous studies document that both species detect λ 's longer than those that are most attractive. We hypothesize that seafinding is a specialized response mediated by cones that are sensitive to the shorter λ 's (to minimize the effects of dark noise) but such as rods, are especially sensitive to low levels of nocturnal illumination.

Keyword Phototaxis · Seafinding · Stimulus filtering · Spectral sensitivity · Hatchling sea turtle

Introduction

Sea turtles deposit their eggs in subsurface nests placed on oceanic beaches. After a 45–55-day incubation period, the embryos break through the egg shell (“hatching”). Over a period of several more days, the turtles (now called hatchlings) collectively dig their way upward toward the beach surface. They subsequently emerge from the nest when the surface sands cool, a response that promotes nocturnal emergence (Bustard 1967; Mrosovsky 1968; Witherington et al. 1990). Their immediate task, accomplished within minutes afterward, is to determine a crawl direction toward the ocean, an orientation response known as “seafinding” (review: Lohmann et al. 1997).

The beach surface is typically uneven, making it difficult for a small turtle to directly see the ocean from a nest

site that may be > 50 m distant from the surf zone. Experiments show that hatchlings use two sets of visual cues to determine a crawl direction. One cue is horizon elevation, the difference in height between a landward view toward the dune (and its associated vegetation) and the lower and unobstructed views in the opposite (seaward) direction (Mrosovsky 1967; Mrosovsky and Shettleworth 1968). The turtles crawl away from higher and toward lower horizons (Limpus 1971; Lohmann et al. 1997). A second cue is a difference in light radiance (“brightness”) between those two views. Stellar and/or lunar illumination is reflected from the ocean surface but absorbed by vegetation on land. The result is that radiance levels toward the ocean exceed those toward land. The turtles respond to that difference behaviorally with a positive phototaxis (Carr and Ogren 1960; Mrosovsky and Shettleworth 1968; Verheijen 1985). Such differences in radiance may be especially important when nests are deposited on beaches bordering low, flat islands where contrasts in horizon elevation between a landward and seaward view are less obvious (Salmon et al. 1992). Finally, hatchlings during seafinding are most sensitive to cues in a horizontally broad (180°) but vertically narrow (– 10 to + 30° high) visual field. That selectivity excludes extraneous

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“overhead” visual stimuli that provide no orientation cues that they can detect, but focus instead upon both brightness and elevation cues useful for determining a seaward crawl direction (Lohmann et al. 1997).

While the cues that promote seafinding have been known for many years, the spectral distribution and intensity of the light wavelengths present at nesting beaches, upon which that orientation response depends, have not been carefully quantified. For example, while a number of studies (reviewed in Lohmann et al. 1997; Fritsches and Warrant 2013) have explored how hatchlings respond to near-UV (Kawamura et al. 2009) and/or visible (Witherington and Bjorndal 1991a) lighting, we know of no studies that have systematically measured the spectral distribution of available nocturnal lighting at nest sites. In addition, no studies have determined or compared behavioral phototaxis thresholds of the turtles to those wavelengths. Instead, experiments have centered on how hatchlings respond to a somewhat arbitrary selection of intensities and wavelengths, some of which are present at nesting sites while others are characteristic of the luminaires associated with coastal development (e.g., Witherington and Bjorndal 1991b). Those lights pose a significant threat to the turtles as they disrupt seafinding. As a result, there is a significant increase in hatchling mortality (Witherington 1997). Though studies of that nature show that some wavelengths are more attractive and/or disruptive of orientation behavior than others, they provide limited insight into how turtles respond to the natural distribution of lighting present at nesting beaches to optimize the accuracy of their seaward orientation.

The purpose of our study was to address those deficiencies. The following three questions were central. (1) What wavelengths and intensities of light at typical Florida East Coast nesting beaches (major rookery sites for nesting marine turtles) are available as cues for hatchling orientation? (2) How sensitive are the turtles to those wavelengths, with sensitivity measured by the minimum radiance that attracts the hatchlings to those light sources (phototaxis thresholds; Young et al. 2012)? Lastly, (3) what do these relationships between stimulus and response tell us about the likely mechanisms that promote seafinding? Our experimental subjects were green turtle (*Chelonia mydas*) and loggerhead (*Caretta caretta*) hatchlings tested on the night they were scheduled to emerge from their nests.

Materials and methods

Field measurements

We used a UDT S471 Optometer (San Diego, California) to measure nocturnal levels of light radiance at two nesting beaches located on the southeastern coast of Florida,

USA: Juno Beach (26.9122 N, 80.0628 W) and Ocean Ridge (26.5135 N, 80.0496 W). Measurements were made using a UDT 222 sensor for wavelengths at 340 and 360 nm, and a UDT 247 sensor for wavelengths between 380 and 600 nm, measured in 20 nm intervals. Both sensor active areas were 1 cm².

Sensors were positioned to measure light levels near the horizon. They were oriented horizontally and elevated ~1 cm above the beach surface, comparable to the location of a hatchling's eyes during its beach crawl. Measurements were made 2–5 m from the dune (and ~50–150 m from the surf zone), a location where females of both species often place their nests. Readings were obtained after each sensor was pointed directly toward the dune or 180° in the opposite direction (toward the sea). Weather conditions were usually clear, with minimal cloud cover.

Measurements were made during new moon, as well as during the full and quarter moon when the lunar azimuth varied between 80°–130°. At that elevation, our measurements at the horizon were sensitive to indirect, rather than direct, lunar illumination.

The Optometer provided data in Watts/s; we converted those values to photons/cm²/s.

Hatchlings

Hatchlings of both species were collected between July and October, 2017 and 2018, either in the afternoon before they emerged or at night, as they emerged from nests on the beach at Boca Raton (26.32 N–26.39 N, 80.07 W) or at Juno Beach. All nests were marked with stakes and signage that indicate the species and deposition date. We inspected nests 45–50 days later to determine if hatchlings were present near the surface (indicating an emergence would probably occur that night). If they were, the entire clutch was removed and placed inside a covered Styrofoam™ cooler filled with a shallow layer of moist sand. They were maintained in an inactive state by storing the cooler in a dark, warm (27–30 °C) laboratory at Florida Atlantic University. Experiments were done that evening, beginning at ~2100 h, and lasted 2–4 h. That period spanned the time when hatchlings of both species most often emerge from their nests (between dusk and midnight; Witherington et al. 1990; Glen et al. 2005).

Experimental protocols

We used a black plexiglas™ Y-maze (Fig. 1) to determine if the hatchlings detected a light stimulus. That stimulus was projected at a specific wavelength as an illuminated circular target, 6 cm in diameter, visible on a wax paper screen glued across a circular opening at the end of each maze arm. The single arm used to present light stimuli during experiments

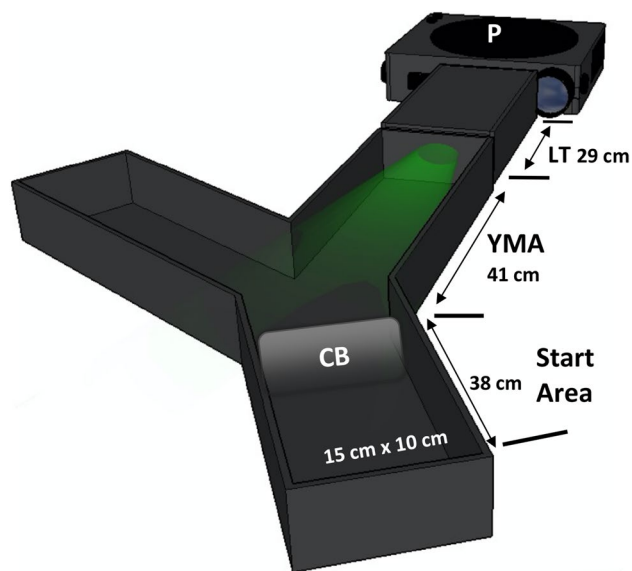


Fig. 1 Diagram of the Y-maze apparatus used to determine the phototaxis thresholds for each light wavelength presented to a hatchling. The turtle is presented with a light from a Kodak projector (P) that casts a circular shape on a frosted wax paper screen affixed at the end of each arm. The stimulus is varied in wavelength and radiance using interference and neutral density filters stacked together in the filter light tunnel (LT). When the light stimulus is presented, the hatchling is restrained in the start area behind a removable clear acrylic barrier (CB). However, it can see the stimulus after it crawls toward the barrier. When the barrier is removed, the turtle can choose between the illuminated and the dark Y maze arm (YMA). A significant preference by a group of turtles for the illuminated arm indicates that the light is detected

was alternated several times during the many evenings required to obtain thresholds, thus eliminating the possibility of a position effect. Each hatchling was tested only once, at one wavelength and intensity. At the end of testing, all the turtles were taken to a dark beach and released.

The Y-maze consisted of a start area (38 cm long \times 15 cm wide) separated by a clear removable acrylic barrier (6.4 mm thick plexiglasTM) from the two arms of identical dimensions (10 cm deep, 41 cm long and 13 cm wide; Fig. 1). Black sandpaper lined the maze floor to provide traction. Each hatchling was placed in the start area of the Y-maze where it could view the visual target through the clear barrier. For a visible light target, the light source was a Kodak® slide projector (Model 440) containing a 300-W tungsten halogen lamp. The near-UV light source consisted of three-stacked 45.7-cm-long 15-W UV “black-light” fluorescent tubes (Chauvet, model NV F-18, Sunrise, Florida, USA) housed in a styrofoamTM cooler (52 \times 36 \times 31 cm high) lined with aluminum foil to enhance reflection. Light escaped through a circular hole in the cooler wall placed against the maze arm that also resulted in a circular UV target, identical in its dimensions to the visible light target.

A light tight plexiglasTM filter tunnel chamber (29.0 cm long \times 12.7 cm wide, inside diameter) was positioned between the maze arm and the light source (Fig. 1). It housed the interference filter (half band pass, 5 nm) used to determine wavelength, and one or more 50 mm square neutral density filters at optical densities of 0.15, 0.3, 0.5, 1.0, or 2.0 (Edmund Optics, Blackwood, New Jersey) used to modify stimulus intensity.

Light radiance generated during each experiment was measured by placing the appropriate UDT sensor inside the maze start area and against the clear acrylic barrier, the location where each turtle initiated its crawl into the Y-maze. The sensor was oriented to obtain a maximum radiance by pointing it directly toward the visual target. Since clear PlexiglasTM only partially transmits light at the near UV wavelengths, it was necessary to determine by how much light radiance was reduced at 340, 360 and 380 nm as it passed through the acrylic barrier. Once that was done, the thresholds at those wavelengths were corrected to reflect the radiance experienced by the turtles after the barrier was removed, and while they made their orientation decisions.

Determining the phototaxis threshold

A sample of 8–15 hatchlings, inactive because they were stored in a warm room in total darkness, was moved into a totally dark, air-conditioned (16–20 °C) laboratory. They were then exposed to a dim “activating” light. Within a few minutes, the turtles were induced to begin crawling and rendered responsive to light stimuli, as would naturally occur after they emerged from their nest. The activating light was extinguished during testing, and while the turtles remained active. When tests scheduled for that evening were done with visible light, the activating light was a dim, near-UV lamp (398 nm, 3.0×10^{09} photons/cm²/s); when tests were done using near-UV lighting, a dim orange–red activating light was used (630 nm, 9.83^{09} photons/cm²/s).

To begin a test, an active hatchling was placed in the start area and exposed to a light stimulus from one maze arm (Fig. 1). The hatchling was given 2 min to crawl toward the clear plastic barrier that separated the start area from the two arms. When it touched the barrier, the barrier was removed so the hatchling could enter one of the two maze arms. A crawl into the illuminated arm was scored as a positive (+) phototaxis. A crawl into the dark arm was scored as a negative (–) phototaxis. Tests were repeated with additional hatchlings until it became evident that the turtles either favored the illuminated arm or were equally likely to enter each arm.

Phototaxis thresholds were obtained using the “up-down-up” staircase method (Dixon and Mood 1948; Cornsweet 1962; Levitt 1971). Experiments began by presenting the light stimulus at an intensity that evoked a clear preference

for the illuminated arm. In subsequent trials, tests were repeated after neutral density filters reduced stimulus intensity, usually in 1.0 log steps, until the preference for the illuminated arm was no longer evident (the “down” portion of the trials). Trials then continued as stimulus intensity was increased, usually in 0.3–0.5 log unit steps, until the preference was re-established (the “up” portion of trials).

Phototaxis thresholds were obtained for each wavelength at 20 nm intervals between 340 and 600 nm. Each threshold was based upon the lowest radiance that attracted a significantly greater proportion of the turtles to the illuminated arm (as determined by a binomial test; Zar 1999). A one-tailed test (at $p \leq 0.05$) was used to determine whether the turtles were significantly attracted to the illuminated arm. That determination required testing many groups of turtles, generally over several evenings, at a variety of stimulus intensities. As a consequence, each phototaxis threshold was based upon the responses of turtles captured that day from a different nest.

Controls

Hatchlings of both species from one nest were exposed to a dim white light of equivalent wattage, projected simultaneously from each arm, to verify that the turtles showed no preference for a particular maze arm (i.e., resulted in a distribution of arm entries indistinguishable from random). Hatchlings were always used only in a single trial to eliminate the possibility that prior exposure to the system could influence subsequent arm choice.

As stated above, the single arm used to present light stimuli during experiments was alternated several times during the many evenings required to obtain thresholds to eliminate the possibility of a position effect.

A hand-held spectrometer (SRI 2000, Allied Scientific Pro, Gatineau, Quebec, Canada) was used to verify that each interference filter remained within ± 3 nm of its designated wavelength throughout the two years required to complete our study.

Results

Field measurements

Radiance measurements were made in 2017 at Ocean Ridge on June 11th (full moon), June 21, (quarter moon), and June 30th (new moon), and at Juno Beach on July 9th (full moon), July 18th (quarter moon) and July 24th (new moon). Artificial lighting, visible as sky glow from an adjacent city (Delray Beach), resulted in elevated radiance levels at Ocean Ridge (Table 1). As expected, radiance measurements were higher during full moon than during either the

quarter or new moon evenings. At both sites, radiance levels in a seaward direction exceeded landward measurements at all wavelengths.

The average level of near-UV radiance (340, 360 and 380 nm) exceeded the average level of visible light radiance (400–600 nm) at both sites, regardless of moon phase (Table 2).

Phototaxis thresholds

A total of 5038 green turtle hatchlings from 55 nests and 1988 loggerheads from 28 nests were used to determine the phototaxis thresholds for each species (Fig. 2).

Hatchlings were attracted to each of the 14 stimulus wavelengths (Table 3). The behavioral thresholds shown by the two species were remarkably similar as both were most sensitive to wavelengths between 360 and 500 nm (Fig. 2). Thresholds at those wavelengths were minimally 2 log units below the light levels measured at the darker site (Juno Beach) during new moon.

Discussion

Field measurements

Our study provides, for the first time, detailed measurements of the lighting present at two nesting beaches on the East Coast of Florida. Ideally, these measurements would be made at locations free from any exposure to coastal development and its attendant sources of artificial lighting. However, few coastal locations in Florida satisfy those criteria while also attracting significant numbers of nesting turtles. We selected Ocean Ridge and Juno Beach as our study sites because the former attracts a low to medium density of nesting turtles while the latter attracts the highest density of nesting turtles per km in the state (in 2017, over 19,085 nests on 11.6 km of beach; <https://www.marinelife.org/nesting-season-17/>).

A measurement of the light spectra present at these “natural” sites, and the changes that occur over time and space, is a first step toward understanding how organisms can exploit their visual environment. Such measurements are known for open terrestrial habitats, under the canopy of forest communities, and for different depths in freshwater and oceanic sites (Cronin et al. 2014). Unfortunately, these data are usually presented as measurements of irradiance (amount of light reaching a certain point from all directions; Fritsches and Warrant 2013; Cronin et al. 2014). During seafinding, hatchlings respond with greatest sensitivity to cues near the horizon and so the more appropriate measurement is radiance (the amount of light coming from a certain direction). We provide this information (Fig. 2; Table 1) with

Table 1 Radiance levels (in photons/cm²/s) measured at Juno Beach (above) and Ocean Ridge (below), Florida, 2017, during comparable phases of the lunar cycle

λ (nm)	Full moon		Quarter moon		New moon	
	Sea	Dune	Sea	Dune	Sea	Dune
Juno Beach, Florida						
340	3.34E+10	2.41E+10	7.22E+09	6.13E+09	4.12E+09	2.88E+09
360	3.57E+10	2.56E+10	7.72E+09	6.58E+09	4.44E+09	3.08E+09
380	2.20E+10	1.26E+10	4.11E+09	3.79E+09	2.35E+09	1.69E+09
400	1.97E+10	1.13E+10	3.71E+09	3.42E+09	2.11E+09	1.53E+09
420	1.99E+10	1.12E+10	3.72E+09	3.43E+09	2.11E+09	1.54E+09
440	2.02E+10	1.20E+10	3.77E+09	3.50E+09	2.16E+09	1.57E+09
460	2.08E+10	1.25E+10	3.89E+09	3.64E+09	2.22E+09	1.61E+09
480	2.15E+10	1.26E+10	4.01E+09	3.72E+09	2.28E+09	1.67E+09
500	2.19E+10	1.26E+10	4.08E+09	3.83E+09	2.32E+09	1.70E+09
520	2.28E+10	1.28E+10	4.21E+09	3.95E+09	2.41E+09	1.76E+09
540	2.34E+10	1.30E+10	4.35E+09	4.10E+09	2.47E+09	1.82E+09
560	2.28E+10	1.27E+10	4.31E+09	4.06E+09	2.41E+09	1.78E+09
580	2.42E+10	1.40E+10	4.58E+09	4.26E+09	2.55E+09	1.88E+09
600	2.60E+10	1.45E+10	4.92E+09	4.56E+09	2.72E+09	2.00E+09
Ocean Ridge, Florida						
340	8.39E+10	3.51E+10	1.59E+10	1.24E+10	7.02E+09	4.79E+09
360	8.75E+10	3.79E+10	1.83E+10	1.33E+10	7.25E+09	4.89E+09
380	6.41E+10	2.33E+10	1.58E+10	1.20E+10	4.21E+09	2.62E+09
400	4.29E+10	1.81E+10	1.43E+10	7.01E+09	4.03E+09	2.42E+09
420	4.36E+10	1.80E+10	1.53E+10	7.02E+09	3.81E+09	2.54E+09
440	4.65E+10	1.97E+10	1.42E+10	7.31E+09	3.99E+09	2.44E+09
460	4.98E+10	1.78E+10	1.46E+10	8.01E+09	3.94E+09	2.55E+09
480	4.88E+10	1.84E+10	1.36E+10	8.17E+09	4.11E+09	2.66E+09
500	5.06E+10	1.84E+10	1.36E+10	8.73E+09	4.28E+09	2.77E+09
520	5.55E+10	1.88E+10	1.38E+10	7.59E+09	4.45E+09	2.88E+09
540	5.74E+10	1.98E+10	1.40E+10	8.16E+09	4.62E+09	3.26E+09
560	5.53E+10	1.95E+10	1.35E+10	7.61E+09	4.51E+09	3.66E+09
580	5.78E+10	2.07E+10	1.40E+10	8.61E+09	4.67E+09	3.21E+09
600	6.10E+10	2.27E+10	1.45E+10	9.54E+09	5.13E+09	3.32E+09

Measurements are separated into near UV and visible light categories

Readings are made when the sensor is oriented seaward or toward the dune (180° apart). Ocean Ridge readings are higher than Juno Beach readings because the former is exposed to more lighting from a near-by town

Table 2 Mean (and percentage) of horizon radiance values measured at Juno Beach and Ocean Ridge

Site	Spectral range	Direction	Full	Lunar phase quarter	New
Juno Beach	UV	Ocean	3.0E+10 (59)	6.4E+9 (54)	3.6E+9 (58)
		Dune	2.1E+10 (41)	5.5E+9 (46)	2.6E+9 (42)
	Visible	Ocean	2.2E+10 (63)	4.1E+9 (51)	2.3E+9 (57)
		Dune	1.3E+10 (37)	3.9E+9 (49)	1.7E+9 (43)
Ocean Ridge	UV	Ocean	7.9E+10 (71)	1.7E+10 (57)	6.2E+9 (60)
		Dune	3.2E+10 (29)	1.3E+10 (43)	4.1E+9 (40)
	Visible	Ocean	5.2E+10 (73)	1.4E+10 (64)	4.3E+9 (60)
		Dune	1.9E+10 (27)	0.8E+10 (36)	2.9E+9 (40)

Percentages are determined by the ocean or dune radiance measurement at any one beach or lunar phase, divided by the summed radiance of both measurements.

Fig. 2 Plots showing the background illumination levels present at a dark nesting site (Juno Beach, Florida), relative to the phototaxis thresholds of the turtles to those wavelengths. Symbols: black circle, green turtles; red circle, loggerheads. Above: radiance measurements at the beach. Values are plotted as pairs (measurements toward the sea; measurements toward the dune) for each series of wavelengths. The brighter seaward measurement is immediately above the dimmer landward measurement under full, quarter and new moon conditions. See Table 1 for the exact radiance. Below: The phototaxis thresholds for the two species, both of which are on average most sensitive to wavelengths between 360 and 500 nm

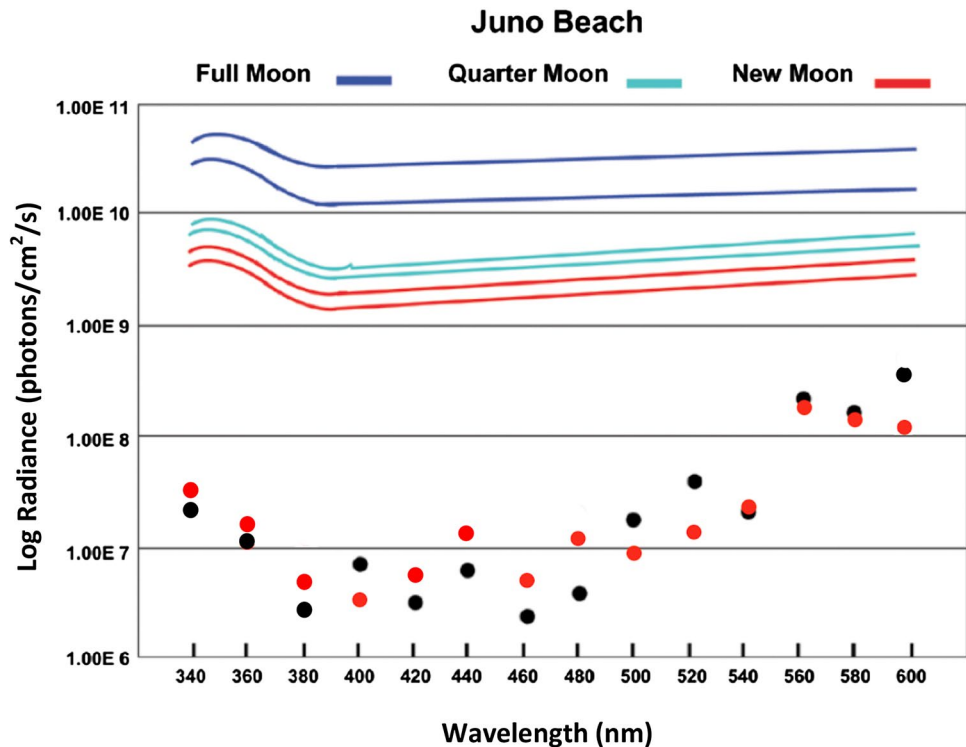


Table 3 Phototaxis thresholds (photons/cm²/s) and response distributions for green turtles and loggerheads

λ (nm)	Green turtles		Loggerheads	
	Threshold	Distribution (+/-)	Threshold	Distribution (+/-)
340	3.37E+7	13/5	4.49E+7	9/1
360	1.39E+7	10/3	1.58E+7	15/6
380	3.74E+6	9/1	6.89E+6	10/3
400	8.46E+6	9/1	4.43E+6	13/5
420	4.04E+6	9/1	5.29E+6	9/2
440	7.09E+6	12/4	1.22E+7	9/1
460	3.24E+6	9/1	5.56E+6	9/2
480	4.83E+6	10/0	1.38E+7	9/1
500	1.56E+7	9/1	9.56E+6	9/2
520	3.64E+7	9/1	1.31E+7	9/2
540	2.10E+7	9/2	2.04E+7	10/3
560	1.58E+8	9/1	1.35E+8	9/2
580	1.35E+8	9/2	1.11E+8	9/2
600	3.97E+8	12/4	1.12E+8	9/2

Phototaxis thresholds are the lowest radiance at that wavelength that attracts a statistically larger number of crawling turtles into the illuminated arm (at $p < 0.05$ by a one-tailed binomial test). For each species, the arm distribution for that wavelength is shown in the column to the right of the threshold column. Symbols: +, turtles entering the illuminated arm; -, turtles entering the dark arm (see Fig. 1).

measurements made toward land, toward the sea, and across a range of wavelengths that are known to attract marine turtles (near UV to 600 nm; Witherington and Bjorndal 1991a; Fritsches and Warrant 2013).

The only other attempt to measure lighting at a nesting beach was made by Kawamura et al. (2009) at the Nagasaki-Bana beach in Kagoshima, Japan. They were specifically interested in documenting the influence of near UV lighting on hatchling orientation, with special emphasis on how lunar illumination might affect seafinding accuracy. Unfortunately, they lacked the equipment required for a direct measurement of UV radiance; instead, they used filters to exclude visible light and UV sensitive film to indirectly record differences in lighting intensity based upon the degree of film exposure. That procedure enabled them to determine that seaward UV light levels always exceeded landward UV light levels during all phases of the lunar cycle. Those findings were consistent with our measurements (Table 1; Fig. 2). In addition, they showed that either a 340- or 370-nm light source, when presented from the side to hatchlings crawling in a seaward direction, caused the turtles to significantly veer in crawl direction toward those light sources. Finally, they did experiments at the beach showing that when given a choice between two light sources (UV at 380 nm; green at 530 nm), hatchlings were differentially attracted to a UV stimulus even when it was presented at a lower wattage. Those results are consistent with other experiments demonstrating that hatchlings (as well as adult turtles) are preferentially attracted to wavelengths at the shorter end of the

spectrum (Mrosovsky and Carr 1967; Ehrenfeld 1968; Mrosovsky and Shettleworth 1968) even though physiologically, turtles can detect light wavelengths that are considerably longer (Granda and O'Shea 1972; Horch et al. 2008).

Why are hatchlings more sensitive to the shorter light wavelengths?

Our phototaxis thresholds for both species (Fig. 2) indicate that green turtle and loggerhead hatchlings are most sensitive to wavelengths between 360 and 500 nm. That result is consistent with other studies showing that the turtles find those wavelengths more attractive than wavelengths exceeding 500 nm (Witherington and Bjorndal 1991a). Why should such a bias occur? It is not immediately obvious from our spectral measurements at the beach what the survival benefits might be. Under water, for example, the rod visual pigments of many open ocean marine vertebrates (fishes and mammals) are tuned to maximize photon capture at the depths where these species tend to forage. As that foraging depth increases, pigment sensitivity tends to shift to the wavelengths that penetrate best to those depths [e.g., Fasick and Robinson 2000]. Comparisons between the spectral sensitivity of two species of marine turtles (loggerhead vs. leatherback (*Dermochelys coriacea*) hatchlings) revealed a somewhat different trend. Both leatherbacks (a deep diving species) and loggerheads (which feed at shallower depths) were maximally sensitive to the same wavelengths (520–540 nm), but leatherbacks were more sharply tuned to wavelengths above and below those frequencies than loggerheads, which were more broadly sensitive to a wider range of wavelengths available at those shallower depths (Horch et al. 2008). Green turtles, which forage in shallow seagrass meadows located in brightly illuminated habitats, are even more uniformly sensitive to a broader range of light wavelengths than loggerheads (Granda and O'Shea 1972).

No such relationship between spectral wavelength distribution, receptor sensitivity and behavioral bias is revealed by our data (Fig. 2; Table 1). We found that nesting beach radiance increased at the shorter (380–360 nm) and more gradually at the longer (400–600 nm) wavelengths. However, the magnitude of those changes was small, that is, less than the differences in radiance associated with changes in lunar illumination. We conclude on that basis that the attraction of the hatchlings to the shorter light wavelengths during seafinding is most likely unrelated to the variation in spectral radiance that occurs at the nesting beach.

An alternative hypothesis is that attraction to the shorter light wavelengths occurs because they present a greater contrast in radiance between the dimmer view landward and the brighter view seaward than do the longer light wavelengths. However, once again our data provide no support for that hypothesis (Table 2). We found that the average difference

in radiance between measurements made toward land and those toward the sea was remarkably consistent (~20%) for both the near UV and visible light wavelengths.

A third possibility, but one not explored in this study, is based upon the inverse relationship between the probability of reliable photon detection under dim lighting conditions (as occurs during seafinding) and thermally induced “dark noise”, defined as the activation of biochemical pathways responsible for receptor response by means other than those produced by photons (Barlow 1956; Baylor et al. 1980; Aho et al. 1988; Warrant 1999). Dark noise interferes with signal detection; its impact on the ability of animals to make reliable discriminations based upon visual contrast can be especially important under dim lighting conditions since certain eyes (like those of marine turtles) are designed to function primarily under bright lighting conditions (Fritsches and Warrant 2013).

Interference by dark noise increases as a function of two factors: longer wavelengths and warmer body temperatures. Because reptiles are poikilotherms whose body temperature at night is on average low, the impact of dark noise effects under dim lighting conditions is typically reduced (Aho et al. 1988; Cronin et al. 2014). But the combined metabolic activity of dozens of hatchlings digging their way out of a nest creates a warm environment that can raise the body temperature of emerging hatchlings between 25 and 28 °C (Mrosovsky 1968), or even higher when substrate temperatures remain elevated (e.g., Drake and Spotila 2002). We hypothesize that the turtles may compensate for those effects by selectively responding to the shorter wavelengths as by doing so, their ability to discern a contrast in radiance and/or elevation between landward and seaward horizons may be enhanced.

Seafinding and UV light detection

In this study, we show that behaviorally, the phototaxis thresholds displayed by green turtle and loggerhead hatchlings to wavelengths between 340 and 600 nm reveal a similar pattern of sensitivity (Fig. 2). Both species were most sensitive to wavelengths between 360 and 500 nm, responding at radiance levels nearly two log units below those measured at Juno Beach during the darkest evenings (new moon). Given that the eyes of marine turtles are not designed for vision under dim light one might assume that these sensitivities in the absence of moonlight are most likely mediated by rod receptors. Green turtle rods have a λ_{\max} (peak absorption area) between 500 and 505 nm (Liebman and Granda 1971) but their photopigment also possesses a second absorption peak (the β -band) that might simultaneously permit UV detection, assuming those wavelengths reached the retina. In green turtles that assumption is likely as the cornea, lens and vitreous allow the transmission of ~70% of

the wavelength energies exceeding 340 nm to that receptor layer (Mäthger et al. 2007). However, given that absorption by the rod photopigment declines between its λ_{\max} and its secondary β -band, it seems unlikely that if vision was mediated by the rods that the turtles would display almost identical phototaxis thresholds between those areas of “best” absorption (Fig. 2).

An alternative hypothesis is that green turtles (and most likely loggerheads) might possess cone receptors that contain a visual pigment with an λ_{\max} in the near UV. Green turtles have cones containing clear oil droplets that are transparent to near UV light (Mäthger et al. 2007). So does a freshwater turtle, the red-eared slider (*Trachemys scripta*). Microspectrophotometric analyses in sliders indicate that the visual pigment contained in those cones has a λ_{\max} at 372 nm (Loew and Govardovskii 2001). Unfortunately in green turtles, the photopigment absorption characteristics of the short-wavelength sensitive cone are currently unknown. A chromatic space model proposed by Schuyler et al. (2014), however, predicts that its peak sensitivity should be at 365 nm.

If, in fact, both green turtles and loggerheads possess cones uniquely sensitive to near UV light, then they could potentially distinguish between objects reflecting UV light from those reflecting short wavelength visible light, detected by cones with an λ_{\max} at 440 nm (Granda and O’Shea 1972). Those receptors in combination with a near UV receptor would render objects reflecting UV vs. short visible light wavelengths as differing in color, and thus provide a cue, in addition to differences in radiance, potentially useful in distinguishing between landward and seaward horizons. Such a capacity could also be favorable to survival and reproductive success in older turtles in a variety of contexts (e.g., selecting appropriate habitats; distinguishing between prey items differing in nutritional value).

What remains to be determined is whether such a UV sensitive cone can respond to the low levels of lighting present at night at marine turtle nesting beaches. Interestingly, Granda and O’Shea (1972) found that cone responses to wavelengths < 520 nm were more easily depressed by an adapting light than cones responsive at longer wavelengths. Transformations in sensitivity among rods and cones are known to occur in reptiles (snakes and geckos; Schott et al. 2016; Simões and Gower 2017; Hauser and Chang 2017) although we know of no reports documenting such occurrences in turtles.

Clearly, our study raises as many questions as it answers.

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Author contributions LC collected the hatchlings and did the experiments with the assistance of two undergraduate students, CS and AF. MS recommend the project and served as an academic advisor. LC and MS wrote the paper.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. This study was permitted by the Florida Fish and Wildlife Conservation Commission (TP 173) and approved by the Florida Atlantic University IACUC Committee (Protocol A16-22).

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