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Thresholds of visible light detection in hawksbill turtle (*Eretmochelys imbricata*) hatchlings

Robert T. Gammariello a,b,* , Stephen G. Dunbar a,b ,

- ^a Marine Research Group, Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, California 92350
- b Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. (ProTECTOR, Inc.), Loma Linda, California 92350

ARTICLE INFO

Keywords: Vision Color Seafinding Lighting Orientation Conservation Beaches

ABSTRACT

Light is the primary environmental cue that hatchling sea turtles use to find the ocean post-emergence from the nest. The process of seafinding is interrupted by any form of light stronger than natural, ambient light. Three of the seven species of sea turtles have been investigated to determine their thresholds of detection for various wavelengths of light across the visible spectrum to help reduce hatchling misorientation. Hawksbill turtles, however, have not yet been investigated, and their general preference for nesting under vegetation, rather than on open sand, justifies the hypothesis that their vision may be more sensitive to lower light intensities than other species. Using a Y-maze choice experiment, we discerned the detection threshold for hawksbill hatchlings for visible light of 415, 470, 535, 555, 590, 601, and 660 nm. Hawksbills were most sensitive to light of 555 nm, least sensitive to light of 660 nm, and exhibited detection thresholds that are intermediate compared to previously studied species of sea turtles. Our results may be critical for informing changes in beachfront lighting, as we illustrate that even at very low intensities, light across the visible spectrum may still attract and misorient hawksbill hatchlings.

1. Introduction

Phototaxis is an organism's response to light cues; moving toward those cues in positive phototaxis or away from those cues in negative phototaxis. Phototaxis in vertebrates has been implicated in aiding the location of mates, avoiding predators, prey finding, and navigation (Aho et al., 1993; Mrosovsky and Boycott, 1966; Lohmann et al., 2017). Habitat, microhabitat, and activity time have all been important correlates of phototactic responses in various organisms (Jaeger and Hailman, 1973; Freiding et al., 2007). Those studies highlight that even closely related species may have different relationships and responses to light based on light intensity, behavior, and habitat features.

Hatchling sea turtles are highly phototactic, typically moving toward the brightest light source (Daniel and Smith, 1947; Ehrenfeld and Carr, 1967; Mrosovsky, 1970). Aside from light intensity, the second component to their seafinding is the angle of light compared to the horizon line (i.e. angle of incidence; Ehrenfeld and Carr, 1967). In their arena experiments conducted in Tortuguero, Costa Rica, Ehrenfeld and Carr tested green hatchlings in either a walled arena which blocked the view of the ocean or an unwalled arena with a view of the ocean. While hatchlings in the unwalled arena crawled toward the ocean as normal,

those in the walled arena did not significantly crawl toward the ocean, and many did not orient in any way, despite orienting seaward when placed in the unwalled arena. Ehrenfeld and Carr (1967) concluded that a view of the horizon was necessary for hatchlings to orient. As such, hatchlings are said to crawl towards the lowest lying brightness cues; typically the light of the moon and stars reflecting off the ocean (Ehrenfeld and Carr, 1967; Mrosovsky, 1970). Seafinding is complicated by human development along nesting beach habitats. Human developments often employ bright lights which can override natural light cues that hatchlings use to navigate, causing them to misorient towards buildings and roadways (Philibosian, 1976; Salmon, 2003), or causing them to become disoriented moving in circles as cues compete (Salmon et al., 1995; Salmon, 2003). Turtle-safe lights have been developed in places, such as Florida, to reduce the number of misorientations and disorientations of the green (Chelonia mydas) and loggerhead (Caretta caretta) turtles nesting there. These lights use either red lights (Long et al., 2022) or Low-Pressure Sodium Vapor (LPS) bulbs which produce a vellow light (Witherington and Martin, 2000). These lights, in combination with shielding, better positioning, and angling of lights, have reduced the numbers of hatchling misorientations and disorientations (Witherington and Martin, 2000; Long et al., 2022). For example, in

^{*} Corresponding author at: Marine Research Group, Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, California 92350. E-mail addresses: rgammariello@students.llu.edu, r.gammariello.jr@sbcglobal.net (R.T. Gammariello), sdunbar@llu.edu (S.G. Dunbar).

their technical report, Witherington and Martin (2000) describe how angling lights away from the beach and positioning lights lower to the ground will reduce the amount of light reaching sea turtle nests. Pendoley and Kamrowski (2016) found that when green and flatback (Natator depressus) hatchlings were exposed to different intensities (250 W and 500 W) and types of light source (High Pressure Sodium Vapor, Metal Halide, and fluorescent) at different distances (100 m, 200 m, 500 m, 800 m) from an arena, hatchlings of both species oriented seaward more frequently when the light source was shielded. Shielding all three light source types had the effect of increasing the effective distance of the light by reducing the amount of light reaching the arena, such that a shielded light at 200 m produced the same hatchling orientation pattern as an unshielded light at 500 m distance. In a study by Long et al. (2022), those authors found that in arena experiments, loggerhead hatchlings oriented seaward when a shielded red LED light was visible from the arena, the same response as when hatchlings were presented with no light in those same arenas. Although these studies have demonstrated various strategies of making lights turtle-safe, what a "turtle-safe" light is may depend on the species affected.

Previous studies on green, loggerhead, and leatherback (*Dermochelys coriacea*) turtle hatchlings have determined the minimum intensity of light to elicit the phototactic response (termed the threshold of detection) for different wavelengths (Celano et al., 2018; Trail and Salmon 2022a). These detection thresholds vary by species, with leatherbacks being the least sensitive (Trail and Salmon 2022a) and greens and loggerheads being approximately equally sensitive with small variations among the species (Celano et al., 2018). For example, leatherback peak sensitivity was 6.3×10^7 photons/cm²/s (photon flux) at 380 nm (Trail and Salmon 2022a), green sensitivity at 380 nm was 3.7×10^6 photon flux, and loggerhead sensitivity at 380 nm was 6.9×10^6 photon flux (Celano et al., 2018), which were not the relative peak sensitivities for greens or loggerheads. The sensitivity of these hatchlings is correlated to the intensity of light from the moon and stars recorded *in situ* from nesting beaches (Trail and Salmon 2022a).

Hawksbill sea turtles (Eretmochelys imbricata) are critically endangered worldwide due to a combination of factors, including habitat loss, illegal harvest, bycatch, illegal wildlife trade, global climate change, and pollution (Meylan and Donnelly, 1999). These factors are exacerbated by the life history of sea turtles in which many hatchlings are produced, yet few (only approximately 1 in 1000 eggs) make it to adulthood (Frazer, 1986), as well as their relatively late onset of maturity, ranging from 15 to 38 years of age (Limpus et al., 2008; Avens et al., 2021). Hawksbills, and indeed all sea turtles, experience their highest rates of mortality within the first year of life, especially during the first few minutes to hours when hatchlings are navigating from the nest to the ocean (a process known as seafinding) then continuing into oceanic currents (Erb and Wyneken, 2019; Oñate-Casado et al., 2021). During this short period of time, hatchlings are consumed by predators (terrestrial, aerial, and marine) or killed by excessive heat if hatchlings emerge during the day (Erb and Wyneken, 2019). Minimizing hatchling mortality during seafinding may lead to increased survivorship into adulthood. This is especially important for critically endangered species, such as the hawksbill sea turtle.

Hawksbill turtles are important in the maintenance of coral reefs across the Caribbean, modifying reef environments by consuming sponges which can overcrowd corals (Meylan, 1988; Dunbar et al., 2008; Berube et al., 2012; Baumbach et al., 2022; Wright et al., 2022). The services hawksbills provide are under threat due to low population numbers. McClenachan et al. (2006) reported a 99.9 % decrease in hawksbill consumption of sponges from historic levels in the Caribbean, and the consumption of these sponges encourages coral reef growth. While the hawksbills of the North Atlantic Regional Management Unit (RMU) are listed as under low risk and threat (SWOT Report 2025), the species as a whole is listed by the IUCN as Critically Endangered (Meylan and Donnelly, 1999). Thus, the maintenance of the North Atlantic RMU, which contains all Caribbean hawksbill populations, is vitally important

since other RMU's globally are under threat or in decline. The Caribbean population of hawksbills is divided into 29 distinct mtDNA populations (Wallace et al., 2023). The population of hawksbills at Sandy Point National Wildlife Refuge (SPNWR) has been monitored since the establishment of the refuge in 1984, although have only become of direct concern in recent years. The hawksbill population at SPNWR is genetically distinct from the nearby and historically important population of hawksbills at Buck Island based on mtDNA (Hill et al., 2018). This is especially noteworthy because the distance between these two nesting sites is only 40 km. Unlike the hawksbill population at SPNWR, that at Treasure Beach is understudied, as are all nesting populations of hawksbills in Jamaica. Due to high nesting numbers, Treasure Beach is likely to be a locally important nesting beach. To date, there has been no official estimation of the contribution of Jamaican hawksbill nesting towards the regional population as a whole.

While other species generally prefer to nest on open sand, hawksbills generally prefer to nest under beach vegetation (Horrocks and Scott, 1991; Kamel and Mrosovsky, 2005). This has led to suggestions that adaptations in hawksbill hatchlings, including smaller overall body size and a more compact body shape, may help to avoid entrapment by roots (Salmon, Reising, and Stapleton, 2016). This nesting preference presents specific challenges that other sea turtle species may not face, as nests are often invaded by roots which can make emergence from the nest more difficult, and roots and leaves below the canopy may present obstacles to hatchling progression towards the ocean (Salmon et al., 2016). Another challenge produced by the nesting biology of hawksbills is that vegetation may essentially block the light which hatchlings require for locating the sea. These challenges provide unique opportunities to investigate hawksbill-specific adaptations and behaviors.

Hawksbill turtles have heretofore not been investigated regarding light detection thresholds. Considering their typical nesting behavior and the reduced light availability under vegetation, it is not unreasonable to suggest they may have evolved more sensitive eyes for the detection of less intense light cues. Due to their general nesting preference, we investigated if hawksbill hatchlings were more sensitive to light at lower thresholds than loggerhead and green sea turtle hatchlings. Understanding the threshold of detection for hawksbills may help inform the creation of turtle-safe lights for implementation on hawksbill nesting beaches with human development, leading to a decrease in incidents of hatchling misorientation, and thereby a decrease in hatchling mortality. Therefore, the overlying objective of this study was to determine hawksbill hatchling thresholds of detection for seven discrete wavelengths of light within the visible spectrum.

2. Materials and methods

2.1. Study site and animal care

Hatchlings were collected on Harvey's Beach in the town of Treasure Beach, St. Elizabeth Parish, Jamaica, and Sandy Point National Wildlife Refuge, St. Croix, U.S. Virgin Islands (Fig. 1). The Treasure Beach site consists of four interconnected beaches separated by rocky headlands. All four beaches had similar beach extent, slope, and cover; beaches were between 5 m and 20 m wide with a gentle slope not exceeding 2 m of elevation. The dominant vegetation was sea grape (*Coccoloba uvifera*), which extended from the sheer cliff that abuts the beach to the water line in some places, although typically stopped approximately 2 m from the high tide line. The dark room at the study site in Jamaica had two windows and a door which were covered by blackout curtains. A table was used as a lab bench on which to situate our experimental apparatus.

The SPNWR consists of three major beaches; North, South, and West, with variations in beach extent, beach slope, and vegetative cover. North Beach has a steep, 2+m berm, with little open sand. Atop the berm is a wide swath of between 30 m to 70 m of *Ipomoea* vines. Behind these vines are tree and bush vegetation consisting predominantly of maho (*Thespesia populnea*), sea grape (*Coccoloba uvifera*), buttonwood

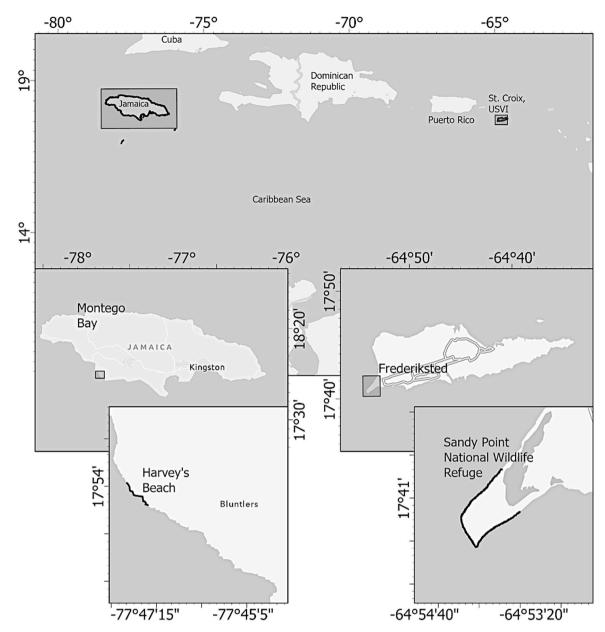


Fig. 1. Map of study site locations. Hatchlings were collected from Treasure Beach, St. Elizabeth Parish, Jamaica and from the Sandy Point National Wildlife Refuge, St. Croix, US Virgin Islands on regular night and morning patrols. Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

(Conocarpus erectus), bay lavender (Argusia gnaphalodes), and bay cedar (Suriana maritima). This denser vegetative zone was located up a secondary berm of approximately 1 m in some parts of the beach. South Beach is a much shallower and gently sloping beach, only ~20 m wide with a rise of only approximately 1.5 m over the extent, before reaching dense vegetation consisting of the same species as North Beach. West Beach is transitional between these two beaches. At the southern end it is shallow and gently sloping, eventually developing a steep berm with large swaths of *Ipomoea* vines toward the north. Depending on erosion and deposition, West Beach may also have a large sand flat without vines and other vegetation. SPNWR is measured in its entire extent from South through West, to North beaches, with markers every 20 m, numbered 1-255. The dark room at the study site in St. Croix had one window and two doors. Doors were covered by blackout curtains, while the window was covered by storm blinds. A table provided the location for our experimental apparatus, similar to the Jamaica site. We collected hatchlings either post-hatching or post-emergence over the course of regular beach patrols both nightly (2000–0230) and every morning (0500–0600). Post-hatchings are here defined as having pipped and emerged from the eggshell, although not from the nest itself, while post-emergence is defined as the hatchling having pipped, emerged from the eggshell, and either emerged from the nest or in the process of emerging from the nest. Hatchlings were then put into a bucket with damp sand and transported to the nearby dark rooms for investigation.

At both locations we confirmed there were no light sources that could be distracting to hatchlings. Hatchlings were maintained in darkness for the duration of holding. Each hatchling was only used in a single trial, after which, the turtle was placed in a separate bucket. Hatchlings collected during morning patrols (0500–0600) were used in trials, kept until that night, and released by 2200 h. Hatchlings collected during night patrols (2000–0230) were used in trials, then released that night by 0300 h.

2.2. Experimental apparatus

We used a Y-maze (Fig. 2) to determine the threshold of detection. The maze was constructed of 10.2 cm diameter PVC pipe with the top half of the pipe removed so that hatchlings could be easily retrieved from within the maze. Each arm of the maze was 0.5 m long; a removable portcullis separated the arms from an antechamber where individual hatchlings were placed to acclimate prior to the start of each trial. At the end of each maze arm was a custom light source that consisted of either four surface-mounted device (SMD) light emitting diodes (LEDs) in the case of the 590 nm light, or six SMD LEDs for all other tested wavelengths. LEDs were arranged on circuit boards (Fig. 3) contained within opaque plastic ammunition boxes. These light boxes connected to the maze via PVC adaptor hubs inserted into the side of the box that channeled light into the maze. Lights were operable at either 5 V or 2 V, depending on the power required to achieve the desired light intensity. Selected wavelengths were obtained through interchangeable circuit boards. We filled the maze with approximately 2 cm of sand to ensure that turtles had a flat, natural-like surface to crawl across, and placed the maze on a turntable allowing it to be randomly oriented with regards to the magnetic field. It was also kept level to ensure that gravitropism was not a confounding variable.

2.3. Experimental procedure

Our experiment tested seven wavelengths of light: 415 (violet), 470 (blue), 535 (green), 555 (green), 590 (yellow), 601 (orange), and 660 nm (red). These wavelengths were chosen as representatives of color ranges throughout the visible spectrum of light while also being similar to wavelengths tested in previous studies (Celano et al., 2018; Trail and Salmon 2022a). We also chose the 590 nm wavelength using an LED to imitate the wavelength created by LPS light sources which are currently used in many turtle-safe lights. Before experimentation began, the light being used in the experiment was turned on for one minute to give it time to warm up. During this time, the seals for the dark room

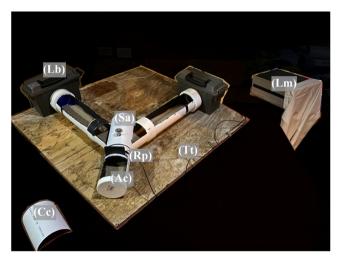


Fig. 2. Y-Maze construction for choice experiments. Hatchlings are placed in the antechamber (Ac) and given 30 s to acclimate. The antechamber is covered with a cover (Cc) to create a completely dark environment for the hatchling. The portcullis (Rp) is pulled after the acclimation period to allow the hatchling to navigate the maze. The sensor apparatus (Sa) is placed at the decision point of the maze, just outside the antechamber, and can be adjusted to point towards the light arm of the maze with the knob on top; it is removed before experimentation. The sensor is connected to the light meter (Lm) which records the intensity of the light coming from the lights located in the light box (Lb). The light meter is covered with a black-out-material sock to prevent light leakage from its screen. The experimental chamber is on top of a turn-table (Tt) so that it can be randomly oriented with regards to the magnetic field.

were checked to ensure there was no light leakage from outside. Once the minute had elapsed, an S247 Sensor Head (Gamma Scientific, San Diego, California) was suspended approximately 1 cm off the sand at the decision point of the Y-maze, pointed towards the light source. This sensor head was connected to a S400 flexOPM Benchtop Optical Meter (Gamma Scientific, San Diego, California), the screen of which was obscured by a black-out material sock to prevent the screen light from interfering with the reading. Light readings were recorded from the optical meter in watts, then converted to photon flux (photons/cm²/s) using the equation:

$$photon flux = \frac{(W/cm^2)}{(h*(c/\lambda))}$$
 (1)

where W = the power reading from the Optical Meter (in W or J/s), cm² is the area of the sensor head (i.e. 1 cm^2), h = Plank's Constant (6.626E-34 J/s), c = speed of light in air (2.998E+8 m/s), and $\lambda = \text{wavelength}$ of light (converted from nm to m). After conversion of the light measurement to photon flux, the sensor head was removed from the maze and trials began.

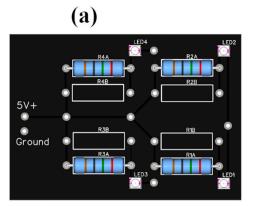
A single active hatchling was randomly selected from the bucket and placed into the antechamber. We closed the antechamber with a lid to give the hatchling 30 s to acclimate to dark conditions, after which point the portcullis was pulled open and the turtle allowed two minutes to navigate through the maze. If the hatchling reached the light end of the maze before the two minutes expired we retrieved the hatchling and logged its position as having gone toward the light. If the hatchling did not reach the end of the maze after two minutes, it's position within the maze was then recorded. If the hatchling was anywhere other than in the light arm of the maze, the hatchling was recorded as not having gone toward the light. However, if after being placed within the antechamber the hatchling did not move, the trial was aborted, the hatchling deemed inactive, and a new hatchling selected. Trials proceeded in groups of ten or eleven according to the up-down staircase statistical method (described below). We used CINIGEL N.9 neutral density filters (NDF) to achieve a 1.0 log unit intensity decrease, and the replacement of a N.9 filter with a ROSCOLUX #97 NDF and #397 NDF to achieve 0.5 and 0.7 log unit increases, respectively.

2.4. Environmental light measurements

In order to contextualize the thresholds of detection that we calculated, we took ambient light measurements on Hawksbill Alley, SPNWR, a high density hawksbill and green turtle nesting beach with vegetation. Ambient light measurements were taken at stake 34, one of the regularly placed beach length markers on South Beach, using a UDT S471 Handheld Power Meter (Gamma Scientific, San Diego, California) fitted with an S247 Sensor Head (for wavelengths 400-700 nm; Gamma Scientific, San Diego, California) or an S222 Sensor Head (for wavelengths 340-380; Gamma Scientific, San Diego, California), with the sensor kept approximately 1 cm off the ground. These measurements were taken every 20 nm from 340 nm to 700 nm at two locations on the beach facing both seaward and landward (180° opposite seaward). The first location was on open sand, representing the typical location for green turtle nesting, while the second location was underneath maho (Thespesia populnea) and behind bay cedar (Suriana maritima), representing typical hawksbill nesting habitat within vegetation at the SPNWR field site. Measurements were taken on six occasions representing three phases of the moon: New Moon (August 4 and September 2, 2024), First Quarter (August 12 and September 11, 2024), and Full Moon (August 19 and September 17, 2024). For these readings, we ensured the moon was between 230° and 260° lunar azimuth.

2.5. Statistical analysis

Hatchlings were tested using the up-down staircase statistical



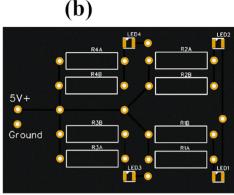


Fig. 3. Example circuit board for LED lights. Fig. 2a shows the front side of the circuit board which has the emitting end of the LEDs, while Fig. 2b shows the reverse side of the circuit board. The board in this figure produces 590 nm light and has four LEDs arranged in series. The circuit boards for the remainder of the lights had six LEDs arranged in series.

method, a dose determination methodology utilizing a series of one-tailed binomial tests. Under this methodology, a group of hatchlings was tested under one light intensity. After the group was tested, a one-tailed binomial test (p-value set at 0.05) was run to determine if the tested light was eliciting a response. If a statistically significant number of hatchlings were orienting toward the light, the intensity was lowered by 1.0 log units. If hatchlings were orienting randomly according to the binomial test, the intensity was raised by either 0.7 or 0.5 log units, based on the previous trial with a 0.5 log unit increase implemented after a 1.0 log unit decrease resulted in random orientation, and a 0.7 log unit increase implemented after a 0.5 log unit increase resulted in random orientation. The next set of hatchlings would be tested under the new light intensity, and another one-tailed binomial test conducted. This continued until phototaxis was re-established, determining threshold.

Because we were able to measure ambient light on only two nights per moon phase, the average for each lunar phase was calculated, although no statistical analyses were possible.

3. Results

Over the course of three field seasons (2022, 2023, and 2024), lasting six weeks, eleven weeks, and eight weeks, respectively, a total of 385 hatchlings were utilized for experimentation from 25 nests. To determine the threshold of detection we tested a range of 20 hatchlings (555 nm) - 120 hatchlings (470 nm) with an average of 55.0 \pm 11.8 hatchlings for a single wavelength.

The threshold of detection varied from 3.41×10^7 photon flux (photons/cm²/s) for 555 nm to 8.72×10^{10} photon flux for 660 nm (Table 1). Therefore, hatchlings were most sensitive to green light of 555 nm and least sensitive to red light of 660 nm. Thresholds for 415 nm, 470 nm, 535 nm, 590 nm, and 601 nm were all within one order of magnitude of each other (Fig. 4).

Table 1List of detection thresholds by wavelength for hawksbill hatchlings with distributions.

Wavelength (nm)	Threshold (photons/cm²/s)	Distribution (+/-)	Hatchlings Used	Clutches Used
415	3.17E+ 8	9/2	53	4
470	6.77E+ 7	10/0	120	9
535	3.67E+8	9/2	51	5
555	3.41E+ 7	9/1	20	1
590	2.73E+ 8	9/1	60	3
601	1.70E+8	10/0	40	2
660	8.72E+ 10	9/2	41	5

Ambient light measurements showed that during all three major moon phases, light levels were lower under vegetation than on open sand (Fig. 4, Supplementary Table 1, Supplementary Table 2, Supplementary Table 3). Light levels were highest during the Full Moon and lowest during the New Moon, regardless of placement on the beach. Hawksbill visual thresholds were below seaward intensities for all wavelengths except 660 nm, regardless of moon phase. Indeed, the threshold for 660 nm was not lower than any lunar illumination level.

4. Discussion

This paper presents the first recordings of hawksbill hatchling detection thresholds for light in the visible spectrum, along with the first recording of a threshold of detection for red light for any species of sea turtle. Our results show that the brightest intensity is required for red light to cause a phototactic response in hawksbills. While this is the first threshold of detection value for any sea turtle species in the red spectrum, it is in accordance with common beachfront lighting practices, as red lights are often employed as "turtle-safe" lights (Long et al., 2022). The other common light employed as "turtle-safe" is Low-Pressure Sodium Vapor (LPS) lights which create a far-yellow color (Witherington and Martin, 2000). We recreated this color in the current study with light of 590 nm. While the threshold for 590 nm was higher than some wavelengths tested (i.e. 601 nm and 555 nm), it did not have the highest, or indeed close to the highest, threshold.

All threshold values were lower than seaward light intensities measured under both vegetation and on open sand under all three moon phases, suggesting that hawksbill vision is adequate for seafinding (Kamel and Mrosovsky, 2005). We do, however, acknowledge that even when sampling under similar cloud cover conditions, as with these measurements, ambient light levels may nevertheless vary. More ambient light measurements over a longer temporal scale would help improve our ability to more fully understand the light levels that are visible from hawksbill nesting sites both on open sand and under vegetation. The one exception to hawksbill thresholds being lower than moonlight is the threshold for 660 nm, which was higher than light produced by Full Moon conditions on open sand. This suggests that hawksbill hatchlings are not using wavelengths of 660 nm for seafinding at night. However, their ability to perceive this wavelength means that it may be important for other phases of their life cycle. For example, Rice (2015) analyzed the photoreceptor distribution of C. mydas and found that photoreceptors did not change over ontogeny in C. mydas. Alternatively, the ability to perceive longer wavelengths may prove beneficial to hawksbill hatchlings which emerge from the nest during times other than at night. Over the course of the current study, hawksbill hatchlings were observed to emerge at all hours of the day and night on both nesting beaches.

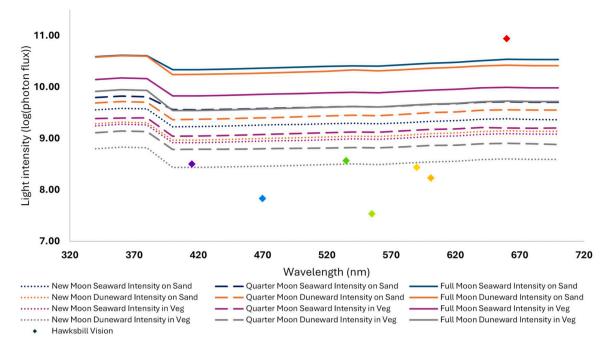


Fig. 4. Hawksbill hatchling detection thresholds by wavelength compared to environmental measures of light intensity. Hatchlings were most sensitive to green light of 555 nm and least sensitive to red light of 660 nm, representing a 1000-fold difference in sensitivity between these wavelengths. The color of the dots above is the color of the light presented to hatchlings. Apart from 660 nm, hawksbill visual thresholds were always below seaward light intensities, both under vegetation and on open sand. This suggests that hawksbill vision is adequate for seafinding, despite the lower light levels present under vegetation.

Results of the current study stand in direct contrast to studies of other sea turtle species. Celano et al. (2018) found that loggerheads and greens were more sensitive to lights of shorter wavelengths, especially as the light neared the ultraviolet spectrum. Similarly, leatherbacks were found to have a higher sensitivity to shorter wavelengths of light (Trail and Salmon 2022a). Our results, however, show that hawksbills are most sensitive to green light, rather than blue or violet. While hawksbills have the lowest detection threshold of any species tested thus far for green light of 555 nm, the remainder of their detection thresholds are intermediate compared to other species with less or equal sensitivity as greens or loggerheads (Celano et al., 2018), and equal or higher sensitivity as leatherbacks (Trail and Salmon 2022a). For example, hawksbill hatchlings tested at 470 nm had a threshold of 6.8×10^7 photon flux, while leatherback hatchlings had a threshold of 1.7×10^8 photon flux at 480 nm, loggerheads had a threshold of 1.4×10^7 photon flux at 480 nm, and greens had a threshold of 4.8×10^6 photon flux at 480 nm. Similarly, hawksbill hatchlings tested at 535 nm had a threshold of 3.7×10^8 photon flux, while leatherbacks had a threshold of 6.4×10^8 photon flux at 540 nm, loggerheads had a threshold of 2.0×10^7 photon flux at 540 nm, and greens had a threshold of 2.1×10^7 photon flux at 540 nm. Trail and Salmon (2022a) suggested that differences in perceptual acuity among species may be due to differences in feeding ecology. Because loggerheads forage in a more structurally complex habitat, looking for more reclusive prey (Bjorndal, 2017; Mariani et al., 2023), they require better vision. This is contrasted with leatherbacks who largely forage in pelagic waters (low structural complexity) and on a specialized group of gelatinous organism prey items, which are slow moving (Saba, 2013). This hypothesis of feeding-ecology-driven vision may be further supported by our data on hawksbill visual thresholds, as hawksbills, while living in a structurally complex habitat (coral reefs) prefer to forage on sessile organisms, namely sponges (Meylan, 1988; Baumbach et al., 2022). This suggests that they do not require especially acute vision to identify prey items, since their prey is not likely to escape detection. However, they do require vision capable of differentiating between sponge species and the surrounding reef, and require vision capable of aiding them in navigating the high structural complexity of a

coral reef. Because we do not know if hawksbills undergo visual changes throughout ontogeny, and we did not measure adult thresholds, this is merely speculation on our part at this time.

The higher detection thresholds for light across the visible spectrum in hawksbill hatchlings (except for green light discussed above) compared to previously tested species of sea turtles does suggest the possibility that these hatchlings use more than one cue for seafinding. This idea is supported by previous studies which have suggested that sea turtles use multiple cues, namely light, slope, and silhouette, in their seaward migration (Van Rhijn, 1979; Salmon et al., 1992). However, light has previously been suggested as the dominant seafinding cue (Daniel and Smith, 1947; Verheijen and Wildschut, 1973; Van Rhijn, 1979). More recent studies by Holtz et al. (2024) have shown that hawksbill hatchlings may deviate from light cues when presented with conflicting wave-crashing sound cues. This is in contrast to individual hatchlings of C. mydas (Holtz et al., 2024), C. caretta (Holtz, 2016), and D. coriacea Holtz et al., 2021), none of which were disoriented by sound cues. The use of sound as a secondary cue may have evolved to compensate for hawksbill poorer vision, rather than evolving higher visual acuity which may be unnecessary for the remainder of their life. It should be noted, however, that hawksbill hatchlings in our study had adequate vision for seafinding under the vegetation conditions that we tested. Secondary cues, such as sound, may become important when nests are situated further in the vegetation where light levels are presumably even lower than where we tested. We were, however, unable to test light levels further into the vegetation to reliably confirm this assumption.

According to threshold data presented here, we suggest that LPS lights make less effective turtle-safe lights for hawksbill nesting beaches, especially when compared with red lights at 660 nm wavelength. Based on the results of our study, we recommend the use of red LEDs as the best hawksbill-safe light for hawksbill-specific nesting beaches. While red lights are currently more difficult to obtain than LPS lights in some locations, such as Florida, LED technology is at the forefront of innovation and is likely to be less expensive and more widely available than current halogen and LPS lighting sources, in time. We continue to emphasize

that while red lights had the highest detection threshold of any color tested, the threshold for this wavelength was still far lower than most beachfront property lights exhibit based on field observations. Presenting the least distracting color is only part of what constitutes a light as "turtle-safe" (Witherington and Martin, 2000). Of equal importance is the position and angle of the light, such that only a minimal amount of anthropogenic light reaches the beach (Witherington and Martin, 2000; Long et al., 2022). Without the combination of all four factors (color, intensity, angle, and position), a high likelihood of hatchling misorientation is maintained.

Future studies are needed to investigate the threshold of detection for hawksbills at the shorter wavelengths of the light spectrum than we tested. The current study focused on a conservation, rather than physiological approach and thus, we did not investigate wavelengths outside the visible spectrum. However, knowledge of hawksbill visual capabilities in the UV spectra is nevertheless important, especially considering the biofluorescent attributes of adult hawksbills (Gruber and Sparks, 2015). Information gathered in this study may be used as a basis for preference experiments, controlling intensity to investigate whether photic energy is the driver of the phototactic response, or if the main driver is wavelength (Trail and Salmon 2022b). This question has been investigated in previous preference studies (Mrosovsky and Carr, 1967; Witherington and Bjorndal, 1991) by keeping intensity of differing colors equal. Results of those studies found that C. mydas and C. caretta hatchlings oriented preferentially toward short wavelengths of light, such as blue or violet. However, considering the different amount of energy required to excite photoreceptor cells within the eye depending on wavelength, it appears prudent to reinvestigate the question of the driver of hatchling phototaxis while factoring in the energy (intensity) required to excite photoreceptors.

Ethical statement

Studies were conducted under the following permits: NEPA permit #18/27 and 18/76 to SGD, USFWS 2024.SPNWR.Dunbar.SUP, DPNR DFW24032U to SGD, and LLU IACUC #815049 to SGD.

CRediT authorship contribution statement

Robert T. Gammariello: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Stephen G. Dunbar:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Robert T. Gammariello reports financial support was provided by Association of Reptile and Amphibian Veterinarians. Robert T. Gammariello reports financial support was provided by The Ocean Foundation. Robert T. Gammariello reports financial support was provided by California Turtle and Tortoise Club. Robert T. Gammariello reports financial support was provided by Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. Stephen G. Dunbar reports financial support was provided by Protective Turtle Ecology Center for Training, Outreach, and Research, Inc. Stephen G. Dunbar reports financial support was provided by California Turtle and Tortoise Club. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Acknowledgements

Financial support for this project was provided by the Association of

Reptile and Amphibian Veterinarians, the Boyd Lyon Memorial Scholarship, the California Turtle and Tortoise Club Inland Empire Chapter, ProTECTOR, Inc., STX Turtles, and the Department of Earth and Biological Sciences at Loma Linda University. We would like to thank Robert Gammariello, Sr., Israel Ko, and Carlos Aguirre for their engineering assistance. Special thanks to Dr. Michael Salmon for discussions of concepts and methods, as well as the use of equipment. Thank you to Josh Derenski for helping with statistics, and to the Treasure Beach Turtle Group, St. Croix Sea Turtles, and Sandy Point Volunteers for their help in obtaining hatchlings. Thank you to Andrea Donaldson and Damany Calder of NEPA, Claudia Lombard of USFWS, and Kelly Stewart of the Ocean Foundation for assistantce in obtaining permits. We also express our deepest thanks to three anonymous Reviewers whose suggestions helped improve the clarity of the manuscript. Studies were conducted under the following permits: NEPA permit #18/27 and 18/ 76 to SGD, USFWS 2024.SPNWR.Dunbar.SUP, DPNR DFW24032U to SGD, and LLU IACUC #815049 to SGD. This is Contribution Number 48 of the Marine Research Group (LLU) and Contribution Number 26 of ProTECTOR, Inc.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104337.

Data availability

Data will be made available on request.

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