

Seafinding by the green turtle, *Chelonia mydas*: the orientation
response is tuned to the lighting environment at the nesting beach

by

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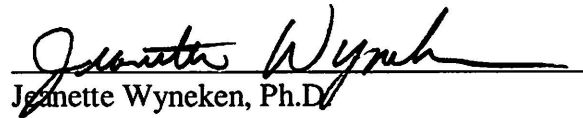
This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Michael Salmon, Department of Biological Sciences, and has been approved by all members of her supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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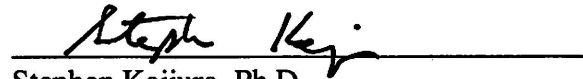


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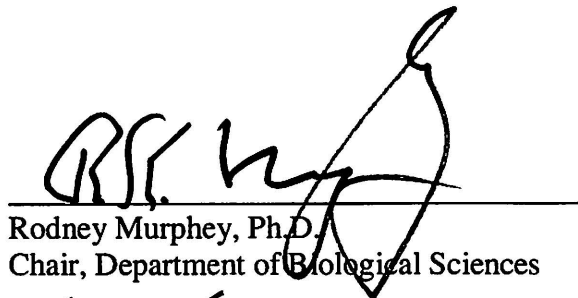
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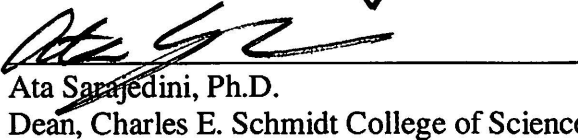


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Abstract

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Hatchling marine turtles use visual cues to orient from their nest to the sea at night. However, the wavelengths of light that carry this information have not been properly documented, nor do we understand why they are favored. I measured wavelength irradiance at 20 nm intervals between 340 – 600 nm at a dark nesting beach and then, in the laboratory, determined the thresholds of the hatchlings for each λ that evoked a positive phototaxis. In this study, I show that green turtle hatchlings are (i) most sensitive to the shorter (360 – 480 nm) light wavelengths. Those light energies (ii) dominated the available natural lighting at the nesting beach. They also (iii) presented a steep gradient in irradiance between a landward and seaward view, an important cue for orientation. I attribute the phototactic responses to “stimulus filtering”, the outcome of natural selection that optimizes behavioral responses (seafinding) according to their function, as well as when and where they occur.

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Introduction

Sea turtles place their eggs in underground nests on beaches above the surf zone. After a 45-55 day incubation period, the turtles escape from the egg, unfold, and dig their way upward toward the beach surface. In most cases, they emerge at night (Bustard, 1967; Mrosovsky, 1968; Witherington et al., 1990). Their task is then to determine which way to crawl to reach the ocean from the nest, an orientation known as “seafinding” (Parker, 1922; Daniel and Smith, 1947; Carr and Ogren, 1960; Ehrenfeld and Carr, 1967; Mrosovsky, 1972). The beach surface is typically uneven, making it impossible for a small turtle to elevate its head high enough to directly see the ocean predictably from the nest site. For that reason, they select a crawl direction based upon visual cues located near the horizon (Mrosovsky, 1967; Mrosovsky and Shettleworth, 1968; van Rhijn and van Gorkom, 1983; Lohmann et al., 1997). They crawl away from an elevated horizon observed in a landward direction, and toward a lower horizon observed in the opposite direction (Limpus, 1971; Salmon and Witherington, 1995). The turtles also use light intensity as a cue as they are attracted to a brighter horizon (star- or moonlight reflected from the water surface) but not the dimmer landward view, darkened because vegetation on the dune absorbs light (Carr and Ogren, 1960; Mrosovsky and Shettleworth, 1968; Verheijen, 1985; Salmon et al., 1992).

These visual cues evolved to optimize seaward orientation at night either in the presence or absence of lunar illumination. However, there is only a superficial understanding of what light wavelengths are actually used by the turtles when making

seafinding orientation decisions. This situation arises because most previous studies have been motivated by problems associated with how the turtles respond to artificial lighting associated with coastal development (Witherington and Bjorndal, 1991a; Bertolotti and Salmon, 2005; Limpus and Kamrowski, 2013). Those light sources disrupt rather than promote seafinding orientation (Verheijen, 1985; Witherington, 1992; Peters and Verhoeven, 1994; Salmon, 2003; Tuxbury and Salmon, 2005). Artificial light sources often are extremely bright and composed of wavelengths that hatchlings may not experience nocturnally at natural nesting beaches. For those reasons, studies of how turtles respond to artificial lighting provides little insight into how hatchlings normally respond to the light wavelengths present at a dark beach.

Physiological studies provide information about what light spectra hatchling or juvenile sea turtles can detect (Liebman and Granda, 1971; Granda and O'Shea, 1972; Horch et al., 2008). These studies established that green sea turtles (*Chelonia mydas*) are sensitive to wavelengths (λ) between 340 – 700 nm. However, sensitivity measurements are primarily useful for determining detection thresholds; they cannot be used with certainty to determine behavioral response patterns under appropriate ecological conditions (Gould, 1982) and in particular, to specify whether a given light wavelength results in a positive or negative orientation response (phototaxis). Natural selection often results in responses to stimuli that most reliably promote survival while at the same time, excluding those stimuli that are irrelevant. This process, known as stimulus “filtering” (Marler and Hamilton, 1966), might reveal that seafinding orientation is a response governed by only a subset of the light wavelengths that hatchling turtles actually detect physiologically.

My purpose in this study was to address this problem by making two kinds of measurements. First, I measured the spectral energies present at night at two nesting beaches, selected as among the darkest of the local available sites. Second, I determined the phototaxis thresholds (Young et al., 2012) of the turtles to the same light wavelengths under controlled laboratory conditions. Those thresholds enabled me to determine which of the wavelengths, measured at the beach, were most likely to be used by the turtles to govern their orientation from the nest to the sea.

Methods

I. Field Measurements

In 2017, I measured the irradiance of light wavelengths available to hatchlings at night at two sites located on the southeastern coast of Florida, U.S.A.: Juno Beach (26.9122 N, 80.0628 W) and Ocean Ridge (26.5135 N, 80.0496 W). (Irradiance is the power/area or density radiant energy/area in W/cm².) The sites were selected because they are minimally exposed to artificial lighting. I used a UDT S471 Optometer (UDT Instruments, San Diego, CA) equipped with a 222 sensor (for UV λ between 340 – 380 nm) or a 247 sensor (for light λ between 400 – 600 nm; both sensor active areas = 1 cm²). Measurements were made at 20 nm increments at similar (80 - 130°) lunar azimuths during full moon, the quarter moon and new moon. The Optometer provides measurements in Watts; I converted these to photons/cm²/s using the following formula:

$$\text{photons/cm}^2/\text{sec} = \frac{\text{Watt} \left(\frac{\text{J}}{\text{s}} \right)}{\frac{\text{cm}^2}{h \cdot \left(\frac{c}{\lambda} \right)}}$$

1 watt (W) = 1 joule/second (J/s)

h = Planck's constant ($6.626 \cdot 10^{-34}$ J/s)

c = Speed of Light ($2.998 \cdot 10^8$ m/s)

λ = wavelength in nm

cm² = Sensor diameter (1 cm²)

At each site, the sensor was elevated ~ 1 cm above the beach surface, a position that mimicked the location of a green turtle hatchling's eyes as it crawled toward the sea. At each λ , I made two measurements: one toward the sea and a second 180° in the

opposite direction, about 5 m from the dune. Weather conditions were always clear with minimal cloud cover.

II. Hatchlings

Green turtle (*C. mydas*) hatchlings were collected between July and October, 2017, as they emerged from nests on the beach at Boca Raton (26.32 N to 26.39 N, 80.07 W) and at Juno Beach, Florida. All nests are marked with stakes and signage that indicated the species and nest deposition date. Nests are monitored through daily surveys by staff who patrol the beach in the morning to find nests deposited the previous evening, and signs of a hatchling emergence from nests deposited 45 – 60 days earlier. I inspected nests I anticipated using 45-47 days after deposition to determine if hatchlings were present near the surface (indicating an emergence would probably occur that night). If they were, I removed the entire clutch from the nest and placed the turtles inside a covered Styrofoam™ cooler filled with a shallow layer of moist sand. The turtles were then transferred to a dark, windowless, non-air-conditioned (27° – 30° C) laboratory at Florida Atlantic University and stored until the evening hours.

III. Laboratory measurements

Green turtles most often emerge from their nests between dusk and midnight (Glen et al., 2005). I began my experiments no sooner than 2100 h. Experiments lasted 2-4 h. Each hatchling was used for a single trial and then released either that night or the next evening at the same beach where it was captured.

I used a 10 cm deep, black Plexiglas® Y-maze (**Appendix A, Figure. 1**) to observe how hatchlings responded to the presence of specific light wavelengths. The Y-maze consisted of a start area (38 cm long x 15 cm wide) at the stem of the Y that led to

two arms of identical dimensions (41 cm long x 13 cm wide). Black sandpaper lined the maze floor to allow for traction. Each hatchling was placed in the start area of the Y-maze where it could see down the length of both maze arms. One arm was dark while the other was illuminated by an image of a 6 cm diameter circle projected on a wax paper screen at the end of the arm. For visible light stimuli, the source was a Kodak® slide projector (Model 440) containing a 300 W tungsten halogen lamp. For UV light stimuli, the source was a Styrofoam™ cooler (52 x 36 x 31 cm) lined with aluminum foil, containing three 15 W UV (peak λ 380 nm) bulbs. Light escaped from the cooler through a circular hole in the cooler wall, and was placed adjacent to the Y-maze arm to present a circular image, identical in its dimensions to the visible light image.

A light tight Plexiglas® filter tunnel chamber (38.5 cm long x 12.7 cm wide inside diameter; **Appendix 1, Figure. 1**) was positioned directly between the maze arm and the light sources. It housed an interference filter (5 nm half band pass; a 400 nm filter would transmit light only between 395 nm and 405 nm, that is, 400 nm +/- 5 nm) and one or more 50 mm square neutral density filters (Edmund Optics, Blackwood, NJ) used to control stimulus wavelength and intensity, respectively. I used 14 interference filters that ranged between 340 – 600 nm at 20 nm increments (**Appendix A, Figure 5**). I used several neutral density filters that had optical densities of 0.3, 0.5, 1.0, and 2.0.

Light stimuli generated during experiments were measured by placing the appropriate Optometer sensor horizontally on the floor of the Y-maze, inside the start area, in contact with the clear barrier, and oriented down the long axis of the illuminated arm. At that location, the sensor was exposed to the stimulus where each turtle made its orientation decision.

IV. Determining phototaxis thresholds

I removed 8-10 turtles from the dark cooler where the entire clutch was stored and generally inactive, into another cooler lined with moist sand. Those turtles were then exposed for several minutes to a dim “activating” light (near-UV or red) and a lower ambient air temperature (16° – 20° C). I used the following procedures to induce hatchling locomotor activity without bleaching the photopigments used to perceive the wavelengths of interest. When determining phototaxis thresholds to visible light wavelengths, I used a LED “black” light headlamp (398 nm at 3.00×10^9 photons/cm²/s) to activate the turtles; when determining phototaxis thresholds to near-UV light wavelengths, I used a red headlamp (630 nm at 9.83×10^9 photons/cm²/s). Both light sources were masked to reduce their intensity, and both soon stimulated the turtles to begin crawling.

To begin a test, I placed an actively crawling turtle in the start area of the Y-maze and immediately exposed it to a light stimulus projected from one maze arm (**Appendix 1, Figure. 1**). The other arm was dark. Each hatchling was given 2 min to crawl down the stem of the Y toward the clear plastic barrier that separated the start area from the arms. When it touched the barrier, I lifted the barrier so the hatchling could enter one of the 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, and a failure to crawl into either arm within 2 min was recorded as a neutral (0) response.

Phototaxis thresholds were obtained using the up-down-up staircase method (Dixon and Mood, 1948; Cornsweet, 1962; Levitt, 1971). Experiments began with the light stimulus presented at an intensity that evoked a clear preference for the illuminated

arm by all of the turtles (typically, 8 – 12 hatchlings, each individually tested) placed in the start area. In subsequent trials, neutral density filters were used to reduce stimulus intensity, usually in 1.0 log unit steps, until the preference for the illuminated arm was no longer statistically significant (the “down” portion of testing) by a binomial test (at $p \leq 0.05$; Zar, 1999). Trials continued as stimulus intensity was once again increased, usually in 0.3 to 0.5 log unit steps, until the preference was re-established (the “up” portion of testing). The phototaxis threshold for that clutch of turtles was defined by the lowest light intensity that evoked a preference for the illuminated arm.

I obtained phototaxis thresholds for each of 14 light wavelengths between 340 – 600 nm. I used turtles from 2 to 6 clutches for each threshold measurement. The lowest threshold obtained from one of those clutches was used to define the threshold to that light wavelength.

V. Controls

To determine if the choice of an arm could be attributed to a stimulus other than the light I presented, I used 30 hatchlings exposed to a dim white light projected at an equal intensity (6.65×10^{11} photons/cm²/s) from each Y maze arm. I used each hatchling in a single trial to eliminate the possibility that prior exposure to the Y-maze and light stimulus might influence how the hatchling responded in subsequent trials.

A hand-held spectrometer (SRI 2000, Allied Scientific Pro, Gatineau, Quebec, Canada) was used to confirm the peak spectral composition of the light stimulus and its bandwidth after it had passed through each interference filter (**Appendix A, Figure 5**).

Results

I. Controls

To determine whether hatchling orientation might be biased toward one of the two windows of the Y-maze, I released 30 green turtles within the Y-maze while both light sources were presented at equal intensity. A total of 13 turtles crawled into the left arm and 17 turtles went right, a distribution that could not be distinguished from random.

The spectrometer readings for the interference filters (**Appendix A, Figure 5**) confirmed that the light stimuli I presented did not deviate more or less than 4 nm of their designated wavelengths.

II. Field Measurements

Irradiance measurements were made at Ocean Ridge, Florida on June 11 (full moon), June 21, (quarter moon), and June 30 (new moon). Measurements were made at Juno Beach, on July 9 (full moon), July 18 (quarter moon) and July 24 (new moon). During the full and quarter moon phases, measurements began when the moon was approximately 23° above the horizon and were completed in about 30 minutes. Artificial lighting was visible as sky glow at both sites, with more glow apparent at Ocean Ridge originating from the adjacent town to the south of Delray Beach. The sky at Ocean Ridge was slightly hazy during full and quarter moon but clear during new moon. At Juno Beach, the weather was clear during full and new moon, and somewhat hazy during the quarter moon.

Irradiance levels were higher under all conditions at Ocean Ridge than at Juno Beach (**Appendix B, Table 1 and 2**). At both sites, irradiance levels out to sea were greater than those measured from a landward direction, regardless of wavelength; they were also greater during full moon than during either quarter moon or new moon illumination. The average level of near-UV irradiance (at 340, 360 and 380 nm) exceeded the average levels of visible light irradiance (400 – 600 nm at 20 nm intervals) at both sites, and regardless of moon phase (**Appendix A, Figure 2**). .

III. Hatchling Phototaxis Thresholds

I used a total of 5,038 hatchlings to determine the phototaxis thresholds at 14 light wavelengths. Hatchlings were attracted to both near-UV (340 – 380 nm) and visible (400 – 600 nm) light stimuli but were most sensitive to light wavelengths between 360 - 480 nm (**Appendix A, Figure. 3; Appendix B, Table 3**). The phototaxis thresholds at those wavelengths were minimally 1 log unit below the light levels measured during new moon at the darker beach site (Juno Beach). The turtles were less sensitive to a 340 nm light, and to wavelengths above 500 nm (**Appendix A, Figure 3**).

Discussion

In this study I assume that the positive phototaxis responses shown by green turtles can be used as a reliable proxy for understanding how light is used for seafinding orientation under natural conditions. The phototaxis thresholds established in this study are clearly biased toward the shorter (360 – 480 nm) light wavelengths that these turtles can detect. However, those are the light wavelengths that are available at nesting beaches, and that are more prevalent in the seaward direction compared to inland. These lighting cues are critical to the hatchlings during seafinding, as they crawl toward the brightest horizon (naturally seaward). In addition, I show that the phototaxis thresholds of green hatchlings are well below the background irradiance levels measured at the beach, especially between 360 and 480 nm where the turtles showed the greatest sensitivity. These results support my hypothesis that seafinding is a behavioral task shaped by natural selection to promote accurate orientation, during the varying natural lighting conditions present under a dark night sky at the beach.

The spectral composition that hatchlings are exposed to at night is characterized (**Appendix A, Figure 3**) in this study. Throughout the lunar cycle, near-UV and visible light wavelengths are present at night, and yield greater intensities in the direction of the ocean than toward the dunes, especially for the near-UV wavelengths. This was consistent for measurements taken at Ocean Ridge and Juno Beach. Similar results were measured by Kawamura et al. (2009), where the near-UV intensity over the sea was greater than that over the land, regardless of the moon's phase or position. While they

lacked equipment sensitive enough to directly quantify UV irradiance, they were able to estimate the intensity using high sensitivity photographic film, where stronger near-UV levels in the seaward direction caused increased bleaching in the film. In this study, I was able to confirm direct irradiance measurements using a UDT Optometer.

Past studies show that hatchling turtles orient toward the sea using a positive phototaxis (Daniel and Smith, 1947; Mrosovsky, 1972; Verheijen and Wildschut, 1973). My results show that hatchlings emerging from nests base this response both upon near-UV and visible light, in the presence or absence of lunar illumination.

Responses to Monochromatic Light

How hatchlings use their visual cues has prompted researchers to investigate their responses to light wavelengths and intensity. However, different approaches yield varying results, even within the same species (**Appendix A, Figure 4**). My findings indicate that green turtle hatchlings orient only to a portion of the λ that they physiologically detect. Green turtles are uniformly sensitive to a broad range of light λ (Granda and O'Shea, 1972); however, behavioral responses in a v-maze show a preference for shorter light wavelengths, including near-UV (360 – 400 nm; Witherington and Bjorndal, 1991b). Different behavioral responses were also observed between species. A previous study on loggerhead hatchlings (*Caretta caretta*) showed that they could detect light wavelengths between 340 - 700 nm (Horch et al., 2008), but yet displayed more complex behavioral responses (attraction, aversion or neutral reactions) to those wavelengths than what I observed for green turtles. Loggerhead and green hatchlings were attracted to lights between 360 - 500 nm, but only loggerheads showed

aversion to green-yellow-orange lights (560 - 600 nm; Witherington and Bjorndal, 1991b).

However, Witherington and Bjorndal (1991b) reported that when intensity was decreased, both species oriented towards all the light wavelengths presented. Similarly, in my study, green turtles were attracted to all the light wavelengths at low intensities. The hatchlings used in Witherington and Bjorndal (1991b) were presented with light passed through eight monochromatic filters, and I expanded on this behavioral study by using 14 filters between 340 – 600 nm. Green turtle hatchlings were attracted to all of the light wavelengths presented, but they oriented to the shorter wavelengths at lower intensity levels than the longer wavelengths.

Monochromatic Light vs. Natural Light

How hatchlings respond to light has generated more recent studies involving the effects of artificial lighting on orientation. If hatchlings are more strongly attracted to the shorter λ , then it could be assumed that eliminating anthropogenic lights of shorter λ , in close proximity to the ocean, should reduce hatchling disorientation. However, most of what is known about hatchling responses to light is limited to findings from manipulating monochromatic light stimuli in lab experiments. These lab studies provide insights into behavior, but it is unlikely that responses to monochromatic light stimuli can be used to comprehensively predict responses to arrays of wavelengths transmitted in nature. When hatchlings emerge from their nests, they are not orienting to the ocean based on a bright light of one color. These limitations aside, the results of this study indicate that hatchlings do display phototaxis to dim light, regardless of the wavelength (near-UV and visible).

Furthermore, hatchling responses to bright anthropogenic light sources cannot be substituted for hatchling responses to natural light cues, because these two sources of light are completely different. Artificial light sources compete with natural lighting and distort the visual cues that hatchlings use (Tuxbury and Salmon, 2005). However, when background irradiance levels are high (under a full moon), the perceived brightness of artificial lighting is diminished (Verheijen, 1985). In the presence of strong artificial lighting, hatchlings either ignore natural light cues or are unable to perceive them as they normally would in the absence of artificial light (Tuxbury and Salmon, 2005). Hatchlings exposed to strong anthropogenic light crawl either in random directions (disorientation) or toward the artificial light source (misorientation; Verheijen, 1985).

A field study in Boca Raton, Florida, showed that when background illumination from the moon reduced the contrast of artificial light sources to natural lighting, loggerhead hatchlings oriented correctly towards the ocean, even though there was more light energy present in a landward direction (Salmon and Witherington, 1995). Alternatively, on moonless nights, artificial sources were more noticeable relative to the background, (increased directivity; Verheijen, 1985) and hatchling orientation was disrupted. Collectively, these responses suggest ‘quality over quantity’, as hatchlings are not orienting exclusively based on brightness. During seafinding, the quality of the natural light produced is evidently more important than the brightest direction (produced by artificial light), as long as the hatchlings are able to perceive correctly. The phototaxis thresholds in my study are accurate because the light stimuli that the hatchlings responded to were extremely dim. Thus, my results are the most likely responses using

monochromatic light stimuli because the observed light intensity at the thresholds was lower than what hatchlings are exposed to at the beach (**Appendix A, Figure 3**).

Electroretinogram (ERG) recordings by Granda and O'Shea (1972) showed that responses varied as a function of light intensity, and an increased sensitivity to the shorter wavelengths was only apparent when the monochromatic test light stimuli were relatively dim. These previous findings, paired with the results from this study, suggest that a heightened sensitivity to the shorter wavelengths under low illumination plays an important role in particular behavioral activities, such as seafinding.

More recently, a field study on leatherback hatchling orientation showed the effect of different light wavelengths (orange, red, blue, green, yellow, and white lights) under the presence and absence of moonlight (Rivas et al., 2015). On moonless nights, hatchlings were either misoriented (blue, green, yellow, and white lights) or disoriented (orange and red lights) in all of the light treatments, yet some hatchlings correctly oriented towards the ocean under orange and red light treatments. These results indicate that the hatchlings were less attracted to, or less distracted by, longer wavelengths (orange and red lights). With moonlight available, misorientation was only observed when hatchlings were exposed to blue and white lights (Rivas et al., 2015). Though the hatchlings tested in my study were not presented with natural moonlight, they exhibited similar phototactic responses in terms of greatest sensitivity to shorter wavelengths (blue) compared to the longer wavelengths (orange – red).

Behavioral Tasks under Dim Lighting

For species active at night, vision may function in a different way, but it is just as important as it is to diurnal animals. Most species have two functionally different visual

systems. One of these (scotopic vision), is optimized for function under dim light, and is mediated by rod receptors and sacrifices visual acuity for object detection. The other (photopic vision), is optimal for function under brighter lighting conditions by cone receptors and accentuates detail (Marler and Hamilton, 1966). Under dim light conditions, humans use rods for vision, and lose their color vision ability. Walls (1934) argued that these photoreceptors (rods and cones) are not fixed, and could potentially evolve into each other (transmutation) due to ecological shifts. It is expected that other animals perceive their visual world differently, but how are they orienting, or seeing color at light intensities that only activate our rods?

Evidence for transmutation was introduced by Walls (1934) through comparisons between diurnal and nocturnal species of geckos and snakes, in which their retinal anatomy displayed a cone-like morphology of rods, and *vice-versa*. For example, the diurnal garter snake (*Thamnophis proximus*) was classified as containing an all-cone retina, although they never actually lost their rods. Instead, the rods evolved into cone-like rods, adapted to a diurnal lifestyle by transmutation (Schott et al., 2016). Nocturnal snakes also support the evolutionary shift of cone transmutation into rod-like structures, as an adaptation to dim light (Simões et al., 2016). It is evident that these functional changes are associated with the photic environment in which species-specific tasks must be accomplished. However, the nocturnal helmeted gecko (*Tarentola chazaliae*) has no rods to see at night, because they are descended from diurnal lizards with an all cone retinae. It is unique how these geckos are active at night, using only cones. The cones in geckos have become more rod-like, with a longer outer segment, which is much more sensitive to light (Roll, 2000). So far, the helmeted gecko is the only nocturnal vertebrate

that possess color vision (transmuted rod-like cones) under dim lighting conditions (Roth and Kelber, 2004). These nighttime adapted visual pigments were also found to be sensitive to shorter wavelengths compared to related diurnal species (Ellingson et al., 1995; Loew et al., 1996). Ancestors of snakes and geckos have experienced significant shifts in diurnal and nocturnal activity patterns, which might justify such changes in the photoreceptors (Schott et al., 2016).

The capacity to possess color vision at night may not be as rare as we might think. Although photoreceptor transmutation has also been found among amphibians (Ma et al., 2001), lampreys (Dickson and Graves, 1979) and skates (Dowling and Ripps, 1990), further research is needed to investigate Wall's theory and the patterns of transmutation. In terms of hatchling sea turtles, it is possible that seafinding is accomplished by using specialized receptors similar to geckos, which do not conform to the usual properties of rods and cones found in mammals.

Sea Turtle Visual Pigments

This study has improved our understanding of how seafinding is accomplished, however how visual pigments are working at night remains somewhat uncertain. The question remains if sea turtles are using rods, cones, or both at night. My study demonstrates that green turtle hatchlings must be using cones (with or without rods) for seafinding orientation under dim lighting conditions. The responses of hatchlings reveal how visual systems are flexible and are modified by the environment in which they live. Yet, given the transitions of reptilian ancestors to and from nocturnal and diurnal lifestyles, the evolution of these visual pigments remains an interesting avenue for future research.

Green turtles possess four classes of photoreceptors: one kind of rod (peak sensitivity at 500-505 nm) and three kinds of cones (Liebman and Granda, 1971; Granda and O'Shea, 1972). The cones show peak sensitivities at 440 nm (blue), 502 nm (blue-green) and 562 nm (green-yellow; Liebman and Granda, 1971). The presence of multiple cones with different pigment sensitivities suggests a strong bias for bright light conditions, and sea turtles are generally diurnal. However, dark-adapted hatchlings, immediately after they emerge from their nest, respond to dim light stimuli in the UV and visible spectrum. Hence, they are responding to dim light λ that are outside of their peak rod sensitivity. The results from this study provide evidence that during seafinding at night, hatchlings are not relying solely on their rods. Furthermore, areas of densely packed cones and ganglion cells, known as the visual streak, are found in sea turtle hatchlings (loggerheads, green turtles, and leatherbacks), and likely enhance visual acuity at the horizon (Oliver et al., 2000). This feature of the cones probably facilitates seafinding, when hatchlings are exposed to open horizons after emergence.

Responses to UV Light

A recent study (Mäthger et al., 2007) suggests that juvenile green turtles also possess a fourth visual cone pigment in the UV range near 325 nm. This would support the findings of previous studies which have found UV vision in a freshwater turtle (*Trachemys dorbignii*; Arnold and Neumeyer, 1987; Ventura et al., 1999). Additional support comes from Fritsches and Warrant (2013) who found that both swimming and crawling loggerhead hatchlings were strongly attracted to UV light wavelengths. Green turtles have also been found to orient behaviorally toward UV light (Witherington and Bjorndal 1991b), including 340, 360 and 380 nm (present study). Hatchling perceptual

thresholds to UV wavelengths were unknown prior to the results presented in my study. A likely benefit for UV sensitivity could be increased foraging ability. Young hatchlings are known to consume planktonic prey, which appears transparent in the visible spectrum, but more detectable in the UV spectrum (Johnsen and Widder, 2001). If sea turtles are able to detect UV light, this would definitely increase their ability to identify prey near the surface. It is also possible that UV vision might aid in other daily tasks such as communication or navigation, but this remains to be investigated.

Visual Ecology and Adaptations

An animal that makes ontogenetic habitat changes may experience adjustments to visual pigments in response to new photic conditions (Crescitelli et al., 1985). As juvenile lemon sharks (*Negaprion brevirostris*) transition to adulthood, they relocate from yellow-green shallow near-shore waters, to blue deeper oceanic waters and experience a shift in peak sensitivity from 522 nm to 502 nm (Cohen et al., 1990). When Atlantic tarpon (*Megalops atlanticus*) approach maturity, there are shifts in photoreceptor spectral sensitivities, including the addition of UV cones (Taylor et al., 2011). Eventually settling in clear waters, the tarpon retinae lose one cone class (~530 nm) and gain three new classes of short-wavelength cones (max ~364, 411, and 476 nm; Taylor et al., 2011). Both species undergo visual pigment modifications as an adaptation response in order to become well suited to their new photic environment.

Green turtle hatchlings are opportunistic feeders that drift within the pelagic environment, and their eventual shift to neritic habitats influences their change in feeding strategies. Although there has been no report of new or lost visual pigments between hatchlings and adults, differences do exist between marine turtle species (Horch et al.,

2008). Yet, adjustments to different habitats and feeding strategies may suggest possible changes in spectral sensitivity from hatchling to adult.

The spectral sensitivities of green turtle hatchlings determined physiologically may be an overall assessment of how vision is optimized across different situations. The behavioral sensitivities presented here suggest that hatchling green turtles may be excluding (stimulus filtering) less important stimuli in order to increase the chances of orienting towards the sea. It is also possible that some light wavelengths are not as important during seafinding, but are relevant later on for other survival functions. Future investigation into how reptiles handle tasks under dim light should lead to a greater understanding of the strategies that have evolved to permit reliable behavior at night. Understanding the effects of evolutionary shifts in the visual environment will further develop insight into the adaptive relevance of visual pigment variation.

I conclude that both UV and visible light wavelengths are probably used by green turtles, and presumably by the hatchlings of other marine turtle species, to locate the sea from the nest. The phototaxic thresholds for green turtles reveal a different sensitivity profile from their receptor sensitivities, suggesting that the seafinding response has been modified by natural selection to promote efficient hatchling orientation. Overall, how sea turtles exploit their visual capabilities and respond to their environment, especially during seafinding, will remain an interesting area to be explored.

Appendices

Appendix A: Figures

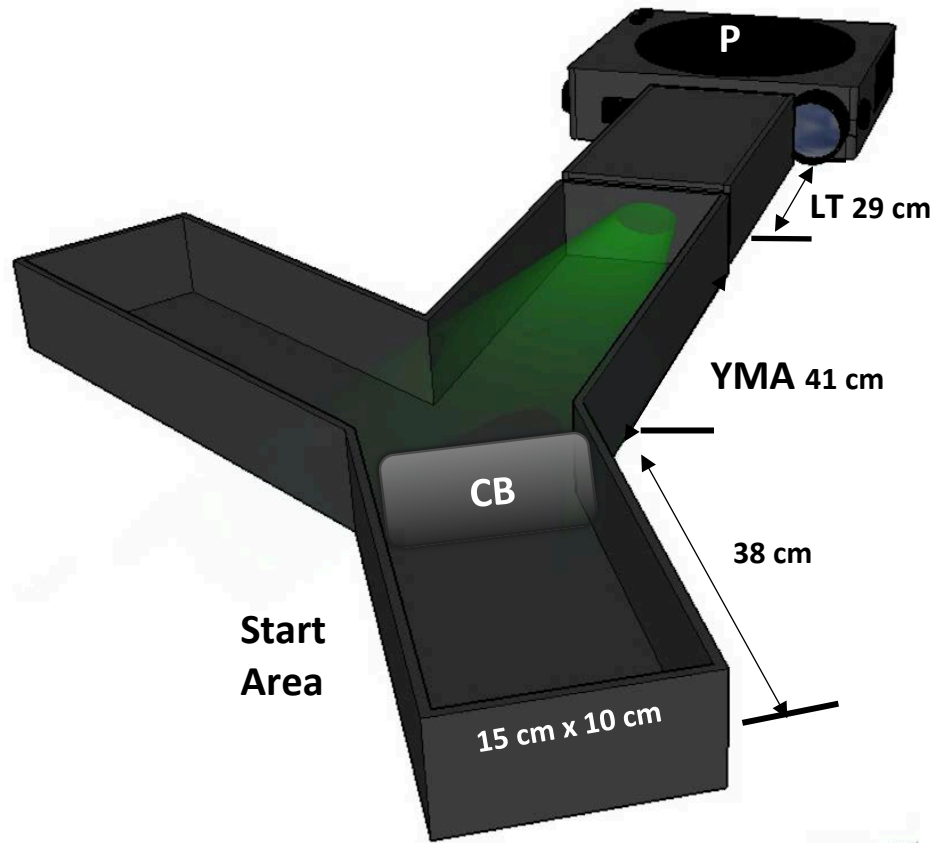


Figure 1. Diagram of the Y-maze apparatus used to determine the thresholds at each wavelength for green turtle hatchlings. The turtle is presented with a light from a Kodak projector for visible light tests and a Styrofoam™ box as a UV source for the UV light tests. The light source (**P**) would cast a circular shape on a frosted barrier at the end of the y-maze arm. The stimulus is varied in wavelength and irradiance using interference and neutral density filters stacked together in the filter light tunnel (**LT**). The turtle is restrained in the start area behind a clear barrier (**CB**) while the light stimulus is presented. However, it can see the stimulus after it crawls toward the barrier. When the barrier is lifted, the turtle can choose between the illuminated and the dark Y maze arm (**YMA**). A preference for the illuminated arm indicates that the light is detected and elicits a positive phototaxis.

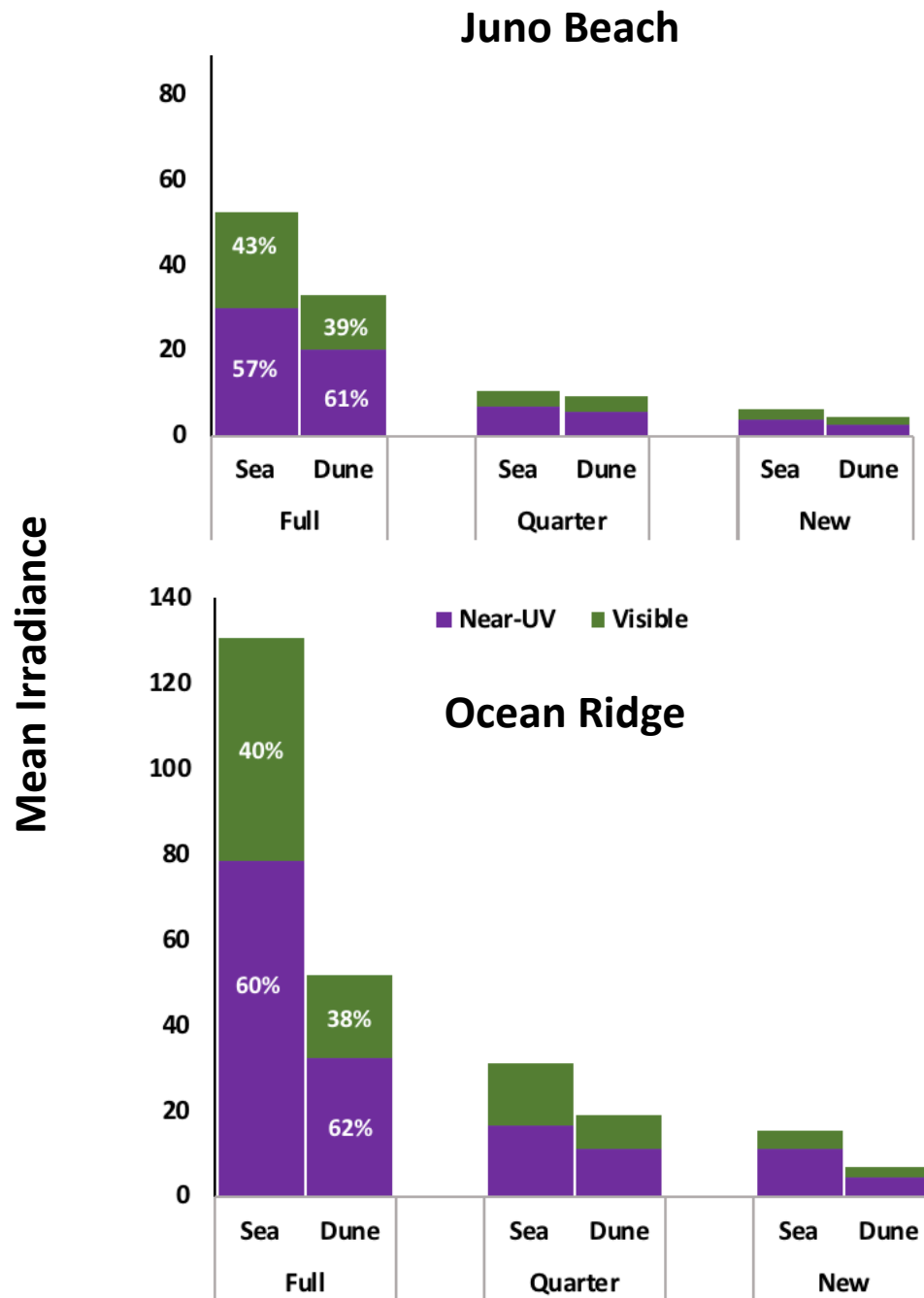


Figure 2. Mean irradiance levels measured at Juno Beach and Ocean Ridge, Florida. Measurements were made towards the sea and toward the dune during the full, quarter and new moon lunar phases. The percentages within bars represent the proportion of near-UV to visible light energies. See **Appendix B, Tables 1 and 2** for the actual irradiance values at each wavelength.

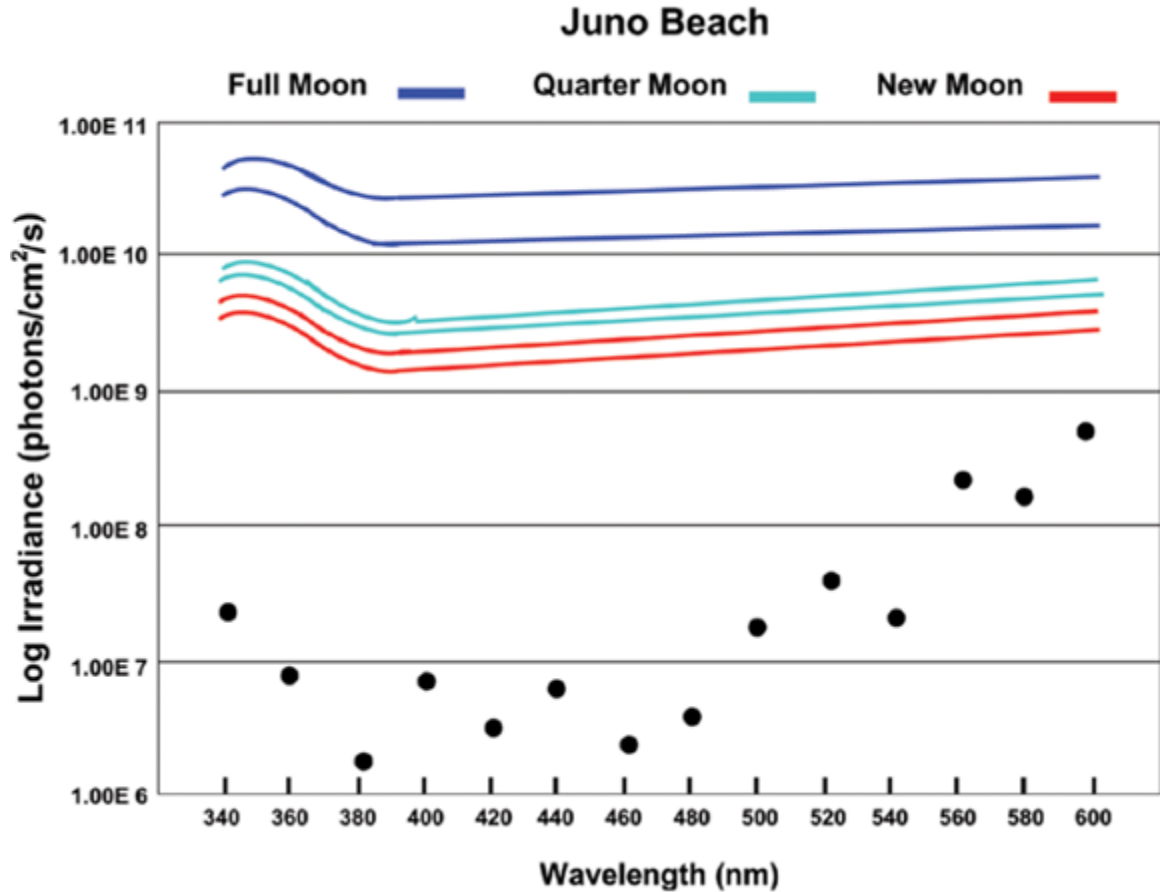


Figure 3. Plots showing the background illumination levels present at a relatively dark nesting site (Juno Beach, Florida), relative to the sensitivity of the turtles to those wavelengths (as measured by their phototaxis thresholds). **Above:** Irradiance measurements at the beach. Values are plotted as pairs: the brighter seaward measurement is immediately above the dimmer landward measurement under full, quarter and new moon conditions. See **Appendix B, Table 1** for the actual irradiance values. **Below:** The phototaxic thresholds, with the irradiance at each wavelength plotted relative to the beach irradiance levels. Actual light intensities at the threshold are presented in **Appendix B, Table 3**.

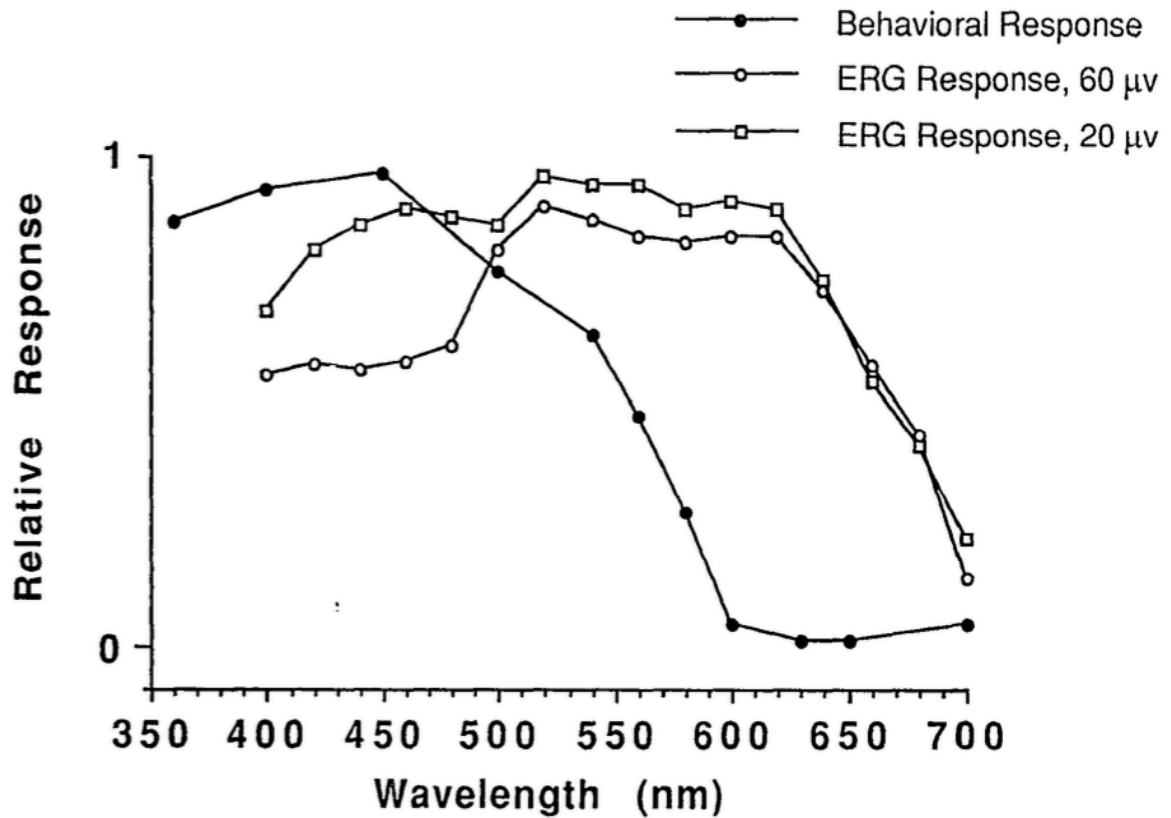


Figure 4. These data compare responses of the visual receptors (open circles and open squares; from Granda and O'Shea 1972) to the behavioral responses of the turtles when exposed to monochromatic lights (1.0 = strong orientation toward the light source; 0.0 = no response to the light; from Witherington and Bjorndal 1991b).

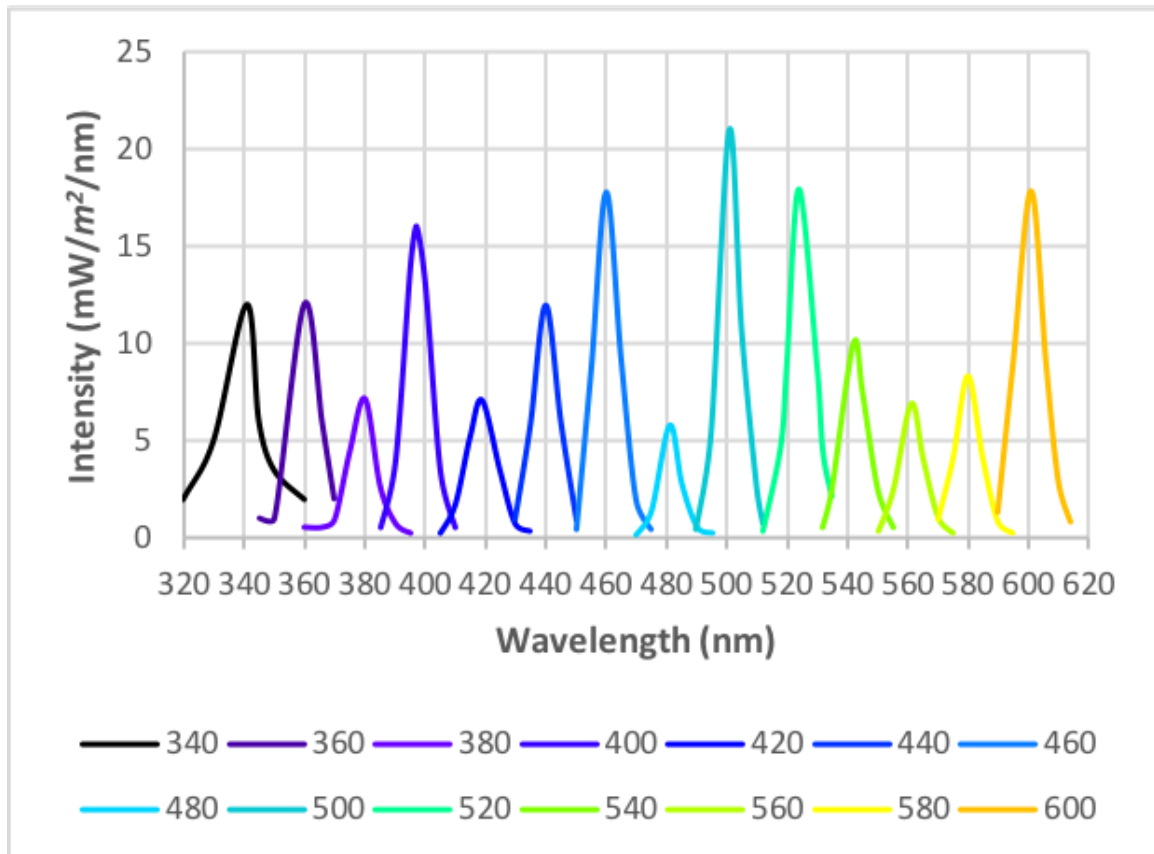


Figure 5. Spectrometer readings for each of the 14 interference filters used to find phototaxis thresholds in this study. Each absorbance peak represents the wavelength (nm) of the light stimulus after it had passed through the corresponding interference filter.

Appendix B: Tables

Table 1. Irradiance levels measured at Juno Beach, Florida, 2017, during comparable phases of the lunar cycle (in photons/cm²/s). Readings are made when the sensor is oriented seaward or toward the dune (180° apart). Compare with Ocean Ridge data (Table 2).

JUNO BEACH, FL						
λ	Full Moon		Quarter Moon		New Moon	
(nm)	Sea	Dune	Sea	Dune	Sea	Dune
340	3.34 x 10 ¹⁰	2.41 x 10 ¹⁰	7.22 x 10 ⁹	6.13 x 10 ⁹	4.12 x 10 ⁹	2.88 x 10 ⁹
360	3.57 x 10 ¹⁰	2.56 x 10 ¹⁰	7.72 x 10 ⁹	6.58 x 10 ⁹	4.44 x 10 ⁹	3.08 x 10 ⁹
380	2.20 x 10 ¹⁰	1.26 x 10 ¹⁰	4.11 x 10 ⁹	3.79 x 10 ⁹	2.35 x 10 ⁹	1.69 x 10 ⁹
400	1.97 x 10 ¹⁰	1.13 x 10 ¹⁰	3.71 x 10 ⁹	3.42 x 10 ⁹	2.11 x 10 ⁹	1.53 x 10 ⁹
420	1.99 x 10 ¹⁰	1.12 x 10 ¹⁰	3.72 x 10 ⁹	3.43 x 10 ⁹	2.11 x 10 ⁹	1.54 x 10 ⁹
440	2.02 x 10 ¹⁰	1.20 x 10 ¹⁰	3.77 x 10 ⁹	3.50 x 10 ⁹	2.16 x 10 ⁹	1.57 x 10 ⁹
460	2.08 x 10 ¹⁰	1.25 x 10 ¹⁰	3.89 x 10 ⁹	3.64 x 10 ⁹	2.22 x 10 ⁹	1.61 x 10 ⁹
480	2.15 x 10 ¹⁰	1.26 x 10 ¹⁰	4.01 x 10 ⁹	3.72 x 10 ⁹	2.28 x 10 ⁹	1.67 x 10 ⁹
500	2.19 x 10 ¹⁰	1.26 x 10 ¹⁰	4.08 x 10 ⁹	3.83 x 10 ⁹	2.32 x 10 ⁹	1.70 x 10 ⁹
520	2.28 x 10 ¹⁰	1.28 x 10 ¹⁰	4.21 x 10 ⁹	3.95 x 10 ⁹	2.41 x 10 ⁹	1.76 x 10 ⁹
540	2.34 x 10 ¹⁰	1.30 x 10 ¹⁰	4.35 x 10 ⁹	4.10 x 10 ⁹	2.47 x 10 ⁹	1.82 x 10 ⁹
560	2.28 x 10 ¹⁰	1.27 x 10 ¹⁰	4.31 x 10 ⁹	4.06 x 10 ⁹	2.41 x 10 ⁹	1.78 x 10 ⁹
580	2.42 x 10 ¹⁰	1.40 x 10 ¹⁰	4.58 x 10 ⁹	4.26 x 10 ⁹	2.55 x 10 ⁹	1.88 x 10 ⁹
600	2.60 x 10 ¹⁰	1.45 x 10 ¹⁰	4.92 x 10 ⁹	4.56 x 10 ⁹	2.72 x 10 ⁹	2.00 x 10 ⁹
Mean:	2.39 x 10¹⁰	1.44 x 10¹⁰	4.61 x 10⁹	4.21 x 10⁹	2.62 x 10⁹	1.89 x 10⁹

Table 2. Irradiance levels measured at Ocean Ridge, Florida, 2017, during comparable phases of the lunar cycle (in photons/cm²/s). Readings are made when the sensor is oriented seaward or toward the dune (180° apart). Compare with Juno Beach data (**Table 1**). Ocean Ridge readings are higher, probably because that site is exposed to more artificial lighting from sky glow and nearby cities.

OCEAN RIDGE, FL						
λ	Full Moon		Quarter Moon		New Moon	
(nm)	Sea	Dune	Sea	Dune	Sea	Dune
340	8.39 x 10 ¹⁰	3.51 x 10 ¹⁰	1.59 x 10 ¹⁰	1.24 x 10 ¹⁰	7.02 x 10 ⁹	4.79 x 10 ⁹
360	8.75 x 10 ¹⁰	3.79 x 10 ¹⁰	1.83 x 10 ¹⁰	1.33 x 10 ¹⁰	7.25 x 10 ⁹	4.89 x 10 ⁹
380	6.41 x 10 ¹⁰	2.33 x 10 ¹⁰	1.58 x 10 ¹⁰	7.23 x 10 ⁹	4.21 x 10 ⁹	2.62 x 10 ⁹
400	4.29 x 10 ¹⁰	1.81 x 10 ¹⁰	1.43 x 10 ¹⁰	7.01 x 10 ⁹	4.03 x 10 ⁹	2.42 x 10 ⁹
420	4.36 x 10 ¹⁰	1.80 x 10 ¹⁰	1.53 x 10 ¹⁰	7.02 x 10 ⁹	3.81 x 10 ⁹	2.54 x 10 ⁹
440	4.65 x 10 ¹⁰	1.97 x 10 ¹⁰	1.42 x 10 ¹⁰	7.31 x 10 ⁹	3.99 x 10 ⁹	2.44 x 10 ⁹
460	4.98 x 10 ¹⁰	1.78 x 10 ¹⁰	1.46 x 10 ¹⁰	8.01 x 10 ⁹	3.94 x 10 ⁹	2.55 x 10 ⁹
480	4.88 x 10 ¹⁰	1.84 x 10 ¹⁰	1.36 x 10 ¹⁰	8.17 x 10 ⁹	4.11 x 10 ⁹	2.66 x 10 ⁹
500	5.06 x 10 ¹⁰	1.84 x 10 ¹⁰	1.36 x 10 ¹⁰	8.73 x 10 ⁹	4.28 x 10 ⁹	2.77 x 10 ⁹
520	5.55 x 10 ¹⁰	1.88 x 10 ¹⁰	1.38 x 10 ¹⁰	7.59 x 10 ⁹	4.45 x 10 ⁹	2.88 x 10 ⁹
540	5.74 x 10 ¹⁰	1.98 x 10 ¹⁰	1.40 x 10 ¹⁰	8.16 x 10 ⁹	4.62 x 10 ⁹	3.26 x 10 ⁹
560	5.53 x 10 ¹⁰	1.95 x 10 ¹⁰	1.35 x 10 ¹⁰	7.61 x 10 ⁹	4.51 x 10 ⁹	3.66 x 10 ⁹
580	5.78 x 10 ¹⁰	2.07 x 10 ¹⁰	1.40 x 10 ¹⁰	8.61 x 10 ⁹	4.67 x 10 ⁹	3.21 x 10 ⁹
600	6.10 x 10 ¹⁰	2.27 x 10 ¹⁰	1.45 x 10 ¹⁰	9.54 x 10 ⁹	5.13 x 10 ⁹	3.32 x 10 ⁹
Mean:	5.75 x 10¹⁰	2.20 x 10¹⁰	1.47 x 10¹⁰	8.62 x 10⁹	4.72 x 10⁹	3.14 x 10⁹

Table 3. Irradiance levels measured at the lowest threshold for each wavelength (in photons/cm²/s). Hatchling response: the number of hatchlings that crawled into the illuminated arm (+), the dark arm (-), or that failed to crawl (0) during the phototaxis trials. The phototaxis threshold is defined as the minimum intensity evoking significant attraction to the light stimulus (at $p \leq 0.05$ by a binomial test).

PHOTOTAXIS THRESHOLDS				
λ	Threshold	Hatchling Response		p value
(nm)	(photons/cm ² /s)	+	-/0	
340	2.34×10^7	13	5	p = .048
360	9.42×10^6	10	3	p = .046
380	2.49×10^6	9	1	p = .011
400	8.46×10^6	9	1/1	p = .033
420	4.04×10^6	9	1/1	p = .033
440	7.09×10^6	12	4	p = .038
460	3.24×10^6	9	1	p = .011
480	4.83×10^6	10	0	p = .001
500	1.56×10^7	9	1	p = .011
520	3.64×10^7	9	1/1	p = .033
540	2.01×10^7	9	2	p = .033
560	1.58×10^8	9	1	p = .011
580	1.35×10^8	9	2	p = .033
600	3.97×10^8	12	4	p = .038

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