Influences of Wavelength and Intensity on Hatchling Sea Turtle Phototaxis: Implications for Sea-Finding Behavior

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Visual cues are important to sea turtle hatchlings in determining seaward direction upon emerging from the nest. In this study, we examined the roles that color and intensity play in the sea-finding mechanisms employed by loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) hatchlings. We tested hatchling preference for a standard source of constant intensity and color (1.26 × 10^{15} photons s^{-1} m^{-2} at 520 nm), versus an adjustable light source (one of five monochromatic colors at each of seven photon intensities), using a two-choice apparatus. Both species oriented toward near-ultraviolet (360 nm), violet (400 nm), and blue-green (500 nm) light but chose the standard light source over yellow-orange (600 nm) and red (700 nm) light. There was a positive relationship between intensity and preference with 360, 400, and 500 nm light. We also examined hatchling choice of either a darkened window or a window lighted by one of eight monochromatic colors at each of two intensities. In these experiments, loggerheads oriented toward 360, 400, and 500 nm light but away from light in the green-yellow to yellow-orange range (560, 580, and 600 nm). Loggerheads oriented toward 700 nm light only at high intensity. Green turtles responded insignificantly to 600 or 700 nm light at either intensity. The contrast of green turtle behavioral responses with published electrophysiological data and the aversion to yellow light observed in loggerheads suggest some level of spectral quality assessment in sea finding for both species.

HATCHLING sea turtles emerge from subsurface nests on oceanic beaches, primarily at night, and immediately move toward the sea. Hatchlings not entering the ocean expeditiously suffer high mortality from predation, exhaustion, and desiccation. The sea-finding behavior of neonate hatchlings occurs to the exclusion of other predator avoidance behaviors. The robust nature of the sea-finding response in sea turtles makes it an excellent model for the study of animal orientation. A detailed description of hatchling sea-finding behavior in the green turtle (*Chelonia mydas*) is given by Carr and Ogren (1960).

Bilaterally blindfolded green turtle (Carr and Ogren, 1960) and loggerhead (*Caretta caretta*; Daniel and Smith, 1947) hatchlings are unable to orient directly toward the sea, providing the best evidence that hatchling sea finding is dependent on visual cues. Green turtle hatchlings also are attracted to artificial light sources (Mrosovsky and Shettleworth, 1968) and lightly tinted objects (Carr and Ogren, 1960) and will move in those directions irrespective of beach slope. The use of vision by sea-finding hatchlings may include an assessment of any combination of the many properties of light detectable by the eye.

Properties of light studied with respect to hatchling orientation include intensity, color, direction, and shape.

Two models predict that sea-finding hatchlings will move in the brightest direction. Brightness in this sense is a measure of intensity having both the directional and spectral sensitivity properties of the hatchling in question. Models describing the mechanism by which hatchlings orient in the brightest direction involve either phototropotaxis (Mrosovsky and Kingsmill, 1985) or a direction system (Verheijen and Wildschut, 1973; van Rhijn, 1979). A third model involves shape as a visual cue (Parker, 1922; Limpus, 1971; van Rhijn, 1979). This model implies form vision and the ability to recognize differences of pattern in the silhouettes of duneward and seaward horizons. Experiments conducted by van Rhijn and van Gorkom (1983) suggest this system may be distinct from, but complementary to, either of the two previous systems.

Spectral quality assessment, or the use of color as a seaward orientation cue also has been suggested (Hooker, 1911; Mrosovsky, 1972). Differential responses to colors may be because of color discrimination as well as a spectral bias

resulting from physiological spectral sensitivity range. Both light intensity and spectral properties play important roles in each of the visual sea-finding mechanisms above. Previous attempts to elucidate the roles of color and intensity in sea turtle hatchling orientation have been limited (Mrosovsky and Carr, 1967; Mrosovsky and Shettleworth, 1968). Primary limitations have been an inability to isolate narrow bandwidths of spectral light and to measure light intensity (e.g., irradiance) at specific wavelengths. Broad-band filters used in earlier studies allow the transmission of many wavelengths and make the assignment of hatchling response to specific colors questionable.

In this paper, we assess preferences for light intensities and narrow bandwidth color sources in loggerhead and green turtle hatchlings during their sea-finding behavior. We evaluate the spectral quality assessment model for hatchling sea finding and suggest a reassessment of models that predict "brightest direction" orientation.

METHODS

Hatchlings.—Loggerhead and green turtle hatchlings for the experiments were taken from clutches transferred into a secured hatchery near Melbourne Beach, Florida, during the summer nesting season, 1988. We examined hatchery nests for signs of hatchling emergence activity at dusk beginning 50 d into incubation (incubation period approximately 50–57 d). Hatchlings typically lie just beneath the surface of the sand until decreasing nighttime temperatures prompt their emergence en masse (Mrosovsky, 1968). We collected hatchlings just after dusk, when they were ready to emerge, and transported them in darkened buckets to an indoor laboratory within 200 m of the hatchery. We kept hatchlings in the dark to ensure that they remained dark adapted and photically naive for experimental trials. Hatchlings were collected and used in experiments during a time when hatchlings are normally emerging and moving to the sea (2100–0200 h, Witherington et al., 1990). Each hatchling was used for a single trial and released the same night on the beach.

Experimental apparatus.—We used a modified T-maze (V-maze) to determine hatchling preference with respect to photic cues (Fig. 1). This apparatus was a V-shaped wooden box, with each identical arm 78 cm in length. Openings
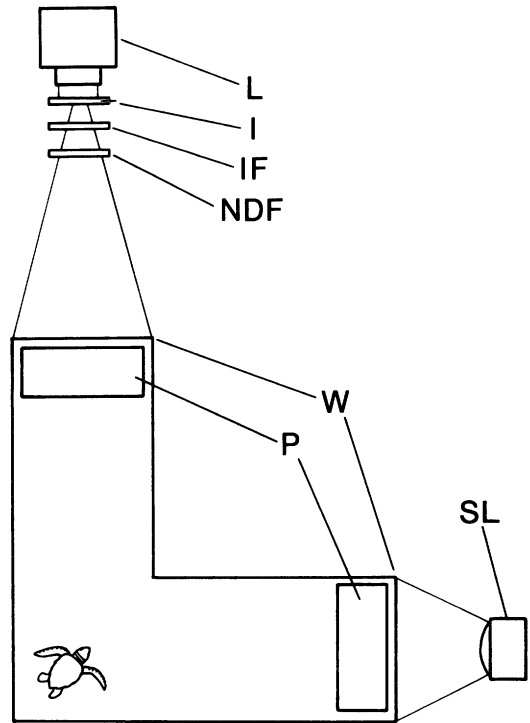

Fig. 1. Schematic diagram of a V-maze used in two-choice, color preference experiments with loggerhead and green turtle hatchlings. L = lamp; I = iris; IF = interference filter; NDF = neutral density filter; W = window; P = pitfall; SL = standard lamp.

at either end of the V-maze were 32 × 32 cm and covered with windows of diffusing acrylic. Black, flocked paper lined the inside of the box. Hatchlings were introduced into the V-maze through a 32 × 32 cm opening in the top of the box near the vertex, which was covered with a black cloth curtain. Hatchlings were covered with an opaque cup that was raised after approximately 20 s to release the hatchling for each trial. We placed hatchlings within the cup so that they pointed toward the midpoint between the two windows, although hatchlings often altered their orientation during the time preceding release. Hatchlings walking from the vertex down either alley of the V-maze would fall into a cloth pitfall pocket at the base of either window.

We positioned two light sources so they shone through each of the two windows of the V-maze (Fig. 1). One of the light sources—hereafter termed standard source—emitted light of constant color (peak emission 520 nm) and intensity

$(1.26 \times 10^{15}$ photons s^{-1} m^{-2} at 520 nm). This source was a conventional tungsten lamp powered with a 3.0 V DC source and fitted with a blue gel filter. We used the blue filter to reduce intensity of the standard source and to make the color of the standard source more easily reproduced. This standard source attracted all hatchlings (n = 20) of each species to a lighted V-maze window when no other light was presented in pretrials. A second source—hereafter termed adjustable source—could be varied in color and intensity. Light for this source originated from a 3200 K (manufacturer's specification) tungsten lamp operated at 115 V AC. We regulated spectral emission of the source with narrow band interference filters (Melles Griot, half bandwidth = 10 nm; transmission outside 20 nm bandpass <0.001%). The angle of the light source beam with the filters was 90° for all trials. We regulated intensity by use of an iris aperture and combinations of neutral density filters (Melles Griot, 3.0, 2.0, 1.0, 0.5, 0.3, 0.1, and 0.04 OD). Intensity was measured as photon flux at the hatchling release point with a LICOR LI-1800 spectroradiometer.

We conducted experiments in a room completely darkened except for the standard and adjustable sources. A series of light baffles prevented light of either source from affecting the other window. Line voltage for the sources was monitored and did not vary more than 1% during experiments.

Treatments.—To determine whether hatchling orientation might be biased toward one of the two windows, we released 42 hatchling loggerheads and 23 hatchling green turtles within the V-maze when both light sources were off. The distribution of loggerhead and green turtle hatchlings falling into pitfalls at either window of the V-maze with both light sources off could not be distinguished from random (alpha = 0.05, binomial probability test, $Z = 0.179$ and $Z = 0.133$, respectively).

To determine the relative preference of hatchlings for light of specific color and intensity, we released hatchlings within the V-maze while respective windows were illuminated with the adjustable source and standard source. In these trials—identified as adjustable source versus standard source—the adjustable source varied among five monochromatic colors and six intensities. Treatment colors were 360 nm (near-ultraviolet), 400 nm (violet), 500 nm (blue-green), 600 nm (yellow-orange), and 700 nm

(deep red) peak transmission. We measured treatment intensities as photon flux and assigned values to a logarithmic scale. Intensities were (log values shown parenthetically) 2.50×10^{14} (0.7), 1.27×10^{15} (1.4), 6.31×10^{15} (2.1), 3.17×10^{16} (2.8), 1.58×10^{17} (3.5), and 1.44×10^{19} (5.5) photons s^{-1} m^{-2} at respective peak wavelengths. Log intensity 0.7 at 500 nm approximated the illuminance level measured for a moonlit night. Higher light levels are comparable to those at dawn or dusk, times at which hatchlings also must locate the sea. Because of the emission spectrum of the incandescent source, the highest log intensity (5.5) could only be reached at the longest wavelengths (600 and 700 nm). We ran one set of trials for each species with the adjustable source off (intensity = 0.0). Combinations of wavelengths and intensities constituted 28 experimental treatments. Thirty loggerhead hatchlings, each from a different clutch, were used individually for each treatment. Ten green turtle hatchlings were used in each treatment and originated from three separate clutches.

To determine the polarity of hatchling response (attraction or avoidance) to light of specific color and intensity, we released hatchlings within the V-maze with one window illuminated by the adjustable source only. In these trials—identified as adjustable source versus darkened window—the standard source window remained dark. We used eight monochromatic colors for the adjustable source in these treatments: 360, 400, 500, 540 (yellow-green), 560 (green-yellow), 580 (yellow), 600, and 700 nm peak transmission. Adjustable source intensity for one set of eight experimental treatments was 3.5 on the log scale. In a second set of eight treatments, we used maximum source intensity, and log intensity of the source varied according to the maximum emission of the incandescent lamp at each wavelength. Maximum intensity of the source at each wavelength was 3.5 (360 nm), 4.0 (400 nm), 4.8 (500 nm), 5.0 (540 nm), 5.2 (560 nm), 5.3 (560 nm), 5.5 (580 nm), 5.5 (600 nm), and 5.7 (700 nm) log units. We ran additional treatments with the adjustable source off for 17 treatments total. Thirty loggerhead hatchlings, three from each of 10 clutches, were run individually per treatment. We used 20 green turtle hatchlings from a single clutch for only the 600 and 700 nm treatments at maximum intensity.

In all trials, we excluded from the analysis hatchlings not falling into either pitfall within

2 min following their release. Less than 10% of the 1523 loggerhead and 384 green turtle hatchlings were excluded. In one to five trials conducted for each treatment, we observed the behavior of hatchlings within the V-maze through the opening at the top of the box. In treatments with both sources darkened, hatchlings were observed through active system night vision goggles using an infrared source mounted above the opening. Data from these trials were not included in the analysis of source preference. Statistical tests for nominal data were used with a null hypothesis rejection criterion of alpha = 0.05.

RESULTS

Hatchling behavior.—In trials resulting in a hatchling choosing one of the two windows of the V-maze, hatchlings exhibited a head-up posture prior to and during movement. Whereas loggerhead hatchlings typically paused prior to moving, green turtle hatchlings were more active, in some cases appearing to move in whatever direction they initially faced. Loggerhead hatchlings moving toward lighted sources typically made direct movements without circling (27 of 29). In trials with both sources off, hatchlings often circled (6 of 10) and made their way to either pitfall by walking along the walls of the box.

Loggerhead hatchlings that fell into the darkened window pitfall in trials with 600 nm light at the adjustable source window did not travel directly to the darkened window. In all of 35 trials observed, hatchlings appeared to turn away from the 600 nm lighted window and walk against the opposite wall, attempting to climb, until they fell into the dark window pitfall. In 30 additional trials, we placed loggerhead hatchlings halfway from the maze vertex to the 600 nm source window (log intensity 3.5) facing the 600 nm source. All of these hatchlings turned away from the lighted window and moved directly to the opposite wall.

Adjustable source versus standard source.—We found a positive relationship between log intensity and the number of loggerhead hatchlings preferring the adjustable source in the shorter wavelength treatments: 360, 400, and 500 nm (Fig. 2). This relationship did not differ among these three treatments (chi-square = 1.86, df = 8). At longer wavelengths, 600 and 700 nm, the number of hatchlings choosing the adjustable source was not statistically different from zero

(binomial probability test) at all intensity levels. With the adjustable source at log intensity 0, all loggerhead hatchlings chose the standard source.

The behavioral response of green turtle hatchlings to spectral light (Fig. 3) was similar to that of loggerhead hatchlings (Fig. 2). Sample sizes do not allow chi-square comparisons between green turtle and loggerhead distributions. Green turtle hatchlings showed little preference for 600 and 700 nm light at any intensity and increasing preference for 360, 400, and 500 nm light with increasing log intensity (Fig. 3).

Adjustable source versus darkened window.—Loggerhead hatchlings chose the window lighted with 360 nm (binomial probability test, Z = 6.25), 400 nm (Z = 6.25), or 500 nm (Z = 5.43) light at log intensity 3.5 significantly more often than the darkened window (Fig. 4a). Conversely, loggerheads presented 560 nm (Z = −5.07), 580 nm (Z = −5.43), or 600 nm (Z = −6.25) light at 3.5 intensity versus a dark window predominantly chose the dark window (binomial probability test). In the 540 nm (Z = −1.02) and 700 nm (Z = 1.30) trials, loggerhead hatchling preference for the adjustable source window or dark window could not be distinguished from random (binomial probability test). Loggerhead preference for the two windows, with the adjustable source at maximum intensity, was significantly different from random in all treatments (360 nm, Z = 6.25; 400 nm, Z = 6.25; 500 nm, Z = 5.43; 540 nm, Z = 3.01; 700 nm, Z = 4.56) except for the 560 nm (Z = 0.08) and 580 nm (Z = 1.35) trials (Fig. 4b, binomial probability test). In trials with 360, 400, 500, 540, or 700 nm light, the lighted window was significantly preferred, but in 600 nm trials (Z = −6.25), all loggerhead hatchlings chose the dark window over the lighted window (binomial probability test).

In the only trials of this type run with green turtles, more hatchlings chose the lighted window when presented 600 nm (n = 14 of 20) and 700 nm (n = 11 of 20) light at maximum intensity, but the distributions cannot be distinguished from random (Z = 1.52 and Z = 0.471, binomial probability test). Loggerhead and green turtle preference for either window of the V-maze in trials with both windows darkened was not different from random (loggerheads, n = 30, Z = 0.520; green turtles, n = 30, Z = 0.252; binomial probability test).
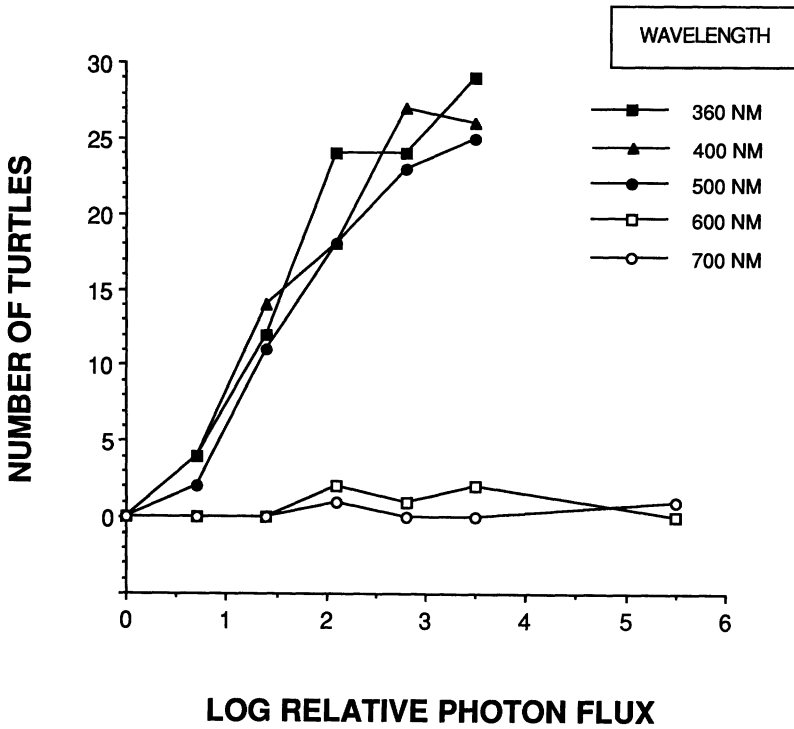
Fig. 2. The number of loggerhead hatchlings out of 30 choosing a light source varying among the wavelengths and intensities specified, over a source of constant color and intensity. All represented hatchlings chose one of the two sources. Colors are near-ultraviolet (360 nm), violet (400 nm), blue-green (500 nm), green (540 nm), green-yellow (560 nm), yellow (580 nm), yellow-orange (600 nm), and deep red (700 nm).

DISCUSSION

Range of spectral sensitivity.—This study gives an indication of a minimal spectral sensitivity range for loggerheads and green turtles. Detailed information on the spectral sensitivity of sea turtles exists only for the green turtle (Ehrenfeld, 1968; Granda and Dvorak, 1977). The action spectrum based on electrophysiological data provided by Granda and O'Shea (1972) shows a greater spectral sensitivity in the shorter wavelengths but does not extend to wavelengths shorter than 400 nm. Work by Ehrenfeld (1968) with green turtles demonstrates that adult females can locate the sea after nesting when fitted with goggles transmitting primarily near-ultraviolet light (300–400 nm). The goggles in these experiments did, however, transmit approximately 1% of the light in the 400 to 700 nm range, a substantial amount for the daytime trials conducted. Because of the narrow spectral bandwidths transmitted by the interference filters we used and the minimal leakage outside

the specified spectral bands, we can assign minimal spectral limits ±10 nm to green turtle and loggerhead vision. We have shown that green turtle vision extends at least from the near-ultraviolet (360 nm) to green (500 nm). Vision in loggerhead turtles extends minimally from the near-ultraviolet (360 nm) to the red (700 nm).

One cannot quantify physiological spectral sensitivities using our preference data because of possible behavioral bias in the way the turtles react to spectral light. A naive analysis of the first series of treatments (Fig. 2), for instance, may discount the ability of loggerheads to see longer wavelengths (600 and 700 nm), an ability demonstrated by the nonrandom choice of the dark window in trials with 600 nm light (Fig. 4a–b) and the lighted window in trials with 700 nm light (Fig. 4b). The nonrandom response of loggerhead hatchlings to 700 nm light only at log intensity 5.7 may indicate that this wavelength borders the spectral sensitivity range of this animal. It is also possible that hatchlings responded to light of other wavelengths trans-
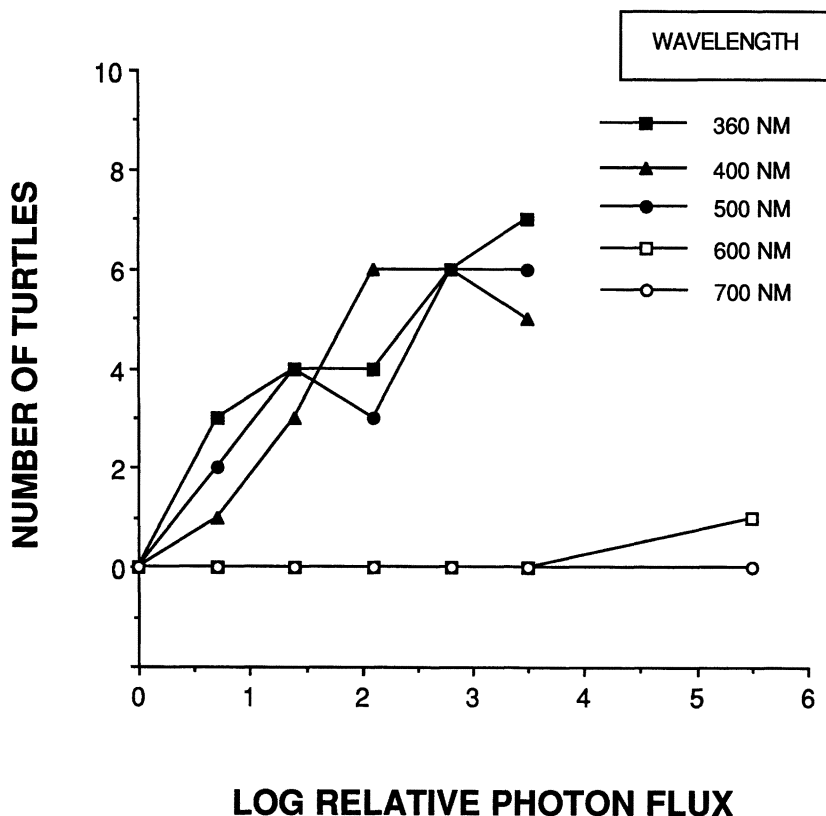
Fig. 3.   The number of green turtle hatchlings out of 30 choosing a light source varying among the wavelengths and intensities specified, over a source of constant color and intensity. All represented hatchlings chose one of the two sources.

mitted by the 700 nm filter, although this light would have been more than four orders of magnitude less intense than the 700 nm light.

In comparison with the pond slider *Trachemys scripta*, vision in sea turtles extends farther into the shorter wavelengths (near-ultraviolet) and, at least in the case of the green turtle, diminishes more abruptly in the longer wavelengths (Granda and Dvorak, 1977). Heightened sensitivity in the near-ultraviolet and other short wavelengths might be characterized as an adaptation for vision in seawater where longer wavelength light attenuates more abruptly with depth (Loew and Lythgoe, 1985).

Spectral light and sea-finding.—A comparison of the green turtle action response measured by Granda and O'Shea (1972) with our measurements of behavioral response to spectral light (Fig. 5) reveals a behavioral bias against longer wavelength light. Care should be taken in draw-

ing conclusions from the comparison in Figure 5. The electroretinogram (ERG) and behavioral data were taken in different ways, although each constitutes a spectral sensitivity of sorts. The ERG curves are adapted from work by Granda and O'Shea (1972) and illustrate light intensities at each color necessary to evoke respective high and low criterion voltage responses at the dark-adapted green turtle eye. The behavioral curve is from the present study and illustrates the number of dark-adapted green turtle hatchlings choosing each color at a single intensity over a light source of standard intensity and color. The behavioral curve is from the data of Figure 3 for log intensity 3.5. The trend shown in Figure 5 is similar for all light intensities in the green turtle behavioral experiments we conducted (Fig. 3). That is, whereas both ERG curves show a peak sensitivity surrounding 600 nm, light in the 600 nm range is relatively unattractive to orienting green turtle hatchlings

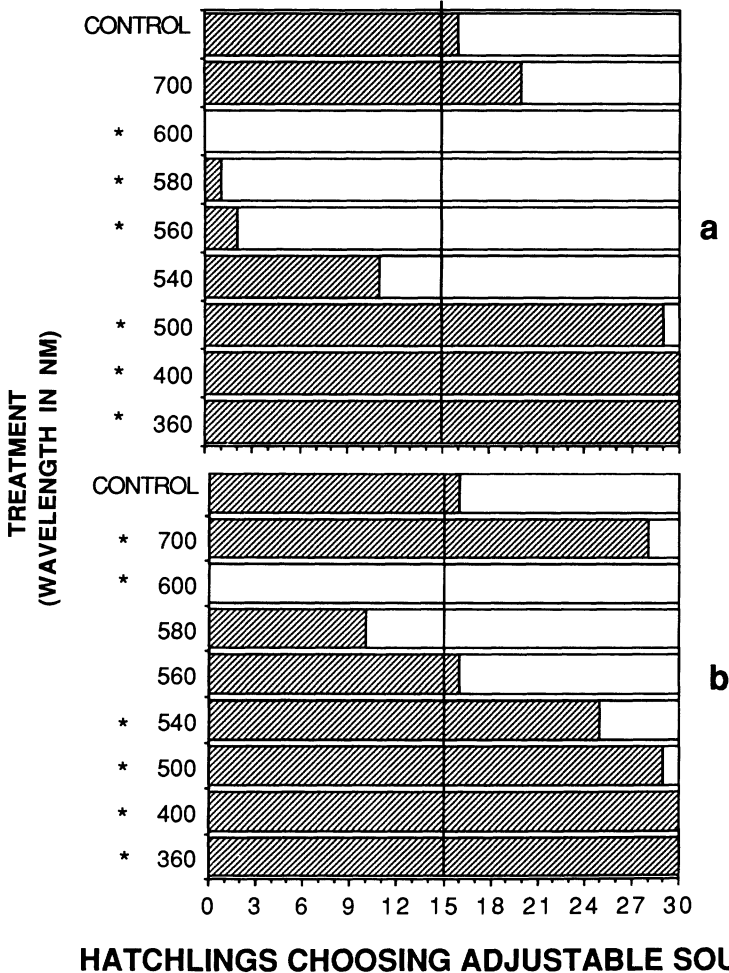**HATCHLINGS CHOOSING ADJUSTABLE SOURCE**

Fig. 4. The number of loggerhead hatchlings choosing an adjustable light source varying among the wavelengths specified, at an intensity of 3.5 log units (a) and at maximum source intensity (b). A darkened window served as the alternate choice. During the control treatment, lighting remained off. All represented hatchlings chose either the darkened window or the light source. Distributions marked with an asterisk (*) are significantly different from random (binomial probability test, $P < 0.05$).

(Fig. 3). This contrast holds when comparisons are made to ERG data taken from light-adapted green turtles as well (Granda and O'Shea, 1972). Mrosovsky (1972), using broad-band blue and red light, also observed discrepancies between behavioral responses of green turtles and the action spectra provided by Granda and O'Shea. Although evidence suggests that green turtle hatchlings use some assessment of spectral quality in sea finding, behavioral experiments that more closely match ERG methods are needed to quantify this pattern.

A phototactic response positively biasing short-wavelength light also has been found among a variety of anurans (Hailman and Jaeger, 1974). Those workers have rejected the contention of Muntz (1962) that the response is an escape mechanism directly resulting in water finding but instead propose an "open sky" attraction hypothesis. In the case of hatchling sea turtles, phototaxis with a spectral bias for short-wavelength light, either reflected from a blue ocean or scattered from a blue sky, may result in seaward orientation under a majority of conditions.

Although no action spectrum exists that would allow a physiological-behavioral comparison to be made for the loggerhead, the manner in
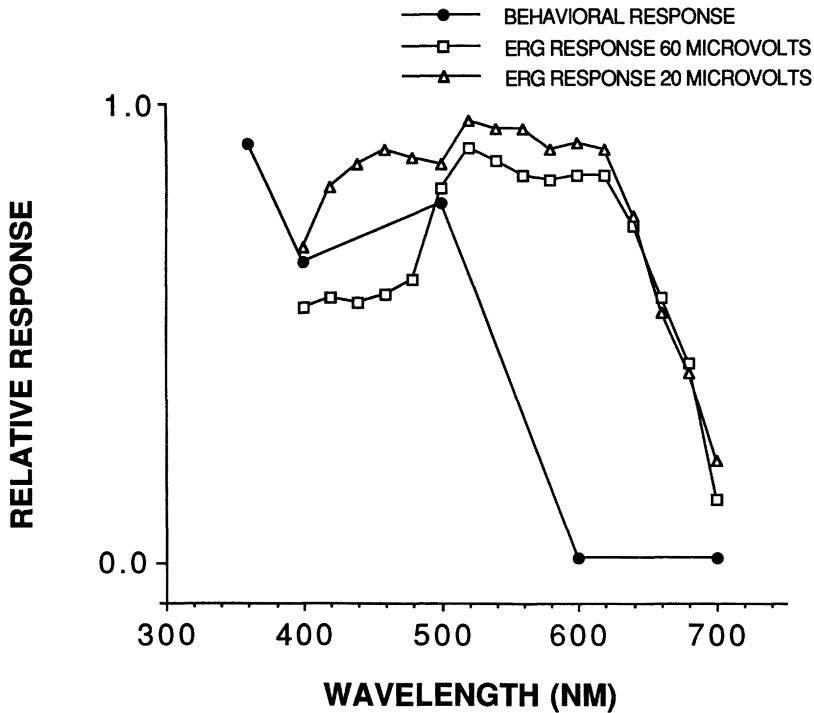
Fig. 5. Behavioral and action responses to spectral light in hatchling green turtles. Relative response for the behavioral curve is the proportion of green turtle hatchlings choosing a light source varying among the wavelengths specified at log intensity 3.5 (1.44×10^{17} photons s^{-1} m^{-1}), over a source of constant color and intensity. Action response curves are adapted from Granda and O'Shea (1972) and represent log sensitivity among wavelengths, as measured by electroretinography (ERG). Relative response for the ERG curves is intensity sufficient to evoke 60 and 20 microvolt criterion responses. The high and low criterion response curves represent high and low light intensity levels. Absolute intensity for the ERG light source was reported to be 2.7×10^{17} photons s^{-1} m^{-2} at 580 nm.

which loggerhead hatchlings behave toward spectral light indicates that they too may use spectral cues in sea finding. Whereas loggerhead hatchlings orient positively to near-ultraviolet, violet, green, and red light (Fig. 2), they avoid yellow and yellow-orange light (Fig. 4a–b). The aversion that loggerhead hatchlings show toward yellow light, or xanthophobic response, has also been observed in loggerhead hatchlings orienting on a natural beach when presented 590 nm monochromatic yellow light from a low pressure sodium vapor (LPS) light source (Witherington and Bjorndal, 1991). Regardless of distance, no loggerhead hatchling was attracted to the LPS light source. In one of the first papers describing sea finding in sea turtles, Hooker (1911) reported that loggerhead hatchlings on a beach during the day responded negatively to panes of glass transmitting primarily orange-red light. Hooker could

not be certain, however, that this response indicated a reaction to color. Responses identical to those Hooker observed are predicted from hatchlings exhibiting simple phototaxis. The responses observed from loggerhead hatchlings in the laboratory (present study) and on the beach (Witherington and Bjorndal, 1991), however, strongly suggest a response to color. If the behavior we observed was simply a response to light of a specified brightness, the same response would have been expected to wavelengths and intensities other than the two intensities of yellow wavelengths (Fig. 4a–b).

A negative response to long-wavelength light (576 and 605 nm) during escape behavior has been reported for the leopard frog (*Rana pipiens*) (Fite et al., 1978). Because the normal escape response of this frog is toward water, this mechanism may share functional similarities with that of the loggerhead. One function

of xanthophobia in loggerhead hatchlings may be to reduce the attraction of light sources with a substantial participation of long-wavelength light. Such an adaptation could be advantageous if long-wavelength light sources with the potential to disrupt the sea-finding ability of a directional or phototropotaxis mechanism were common in nature. Rising and setting celestial bodies appear as predominantly long-wavelength sources because of the short-wavelength scattering effect of the atmosphere and have the potential to disrupt hatchling sea finding. Some controversy exists regarding whether the rising sun affects sea finding in sea turtles. Whereas Ehrenfeld and Carr (1967) and van Rhijn (1979) report that green turtles and hawksbill turtles (Eretmochelys imbricata) are affected insignificantly by the sun on the horizon, Mrosovsky (1970) and Mrosovsky and Kingsmill (1985) report that loggerhead, green, and hawksbill turtles are significantly affected. The loggerhead hatchlings in Mrosovsky's study orienting at sunrise or sunset without the contrast of a dune horizon still moved in the general ocean direction. It is remarkable that the sun, as an intense opposing light source, affected orientation in these experiments as little as it did.

The positive response of loggerhead hatchlings to 700 nm light at high intensity shows that a comprehensive bias against long-wavelength light does not exist. In addition to being on the periphery of color sensitivity in loggerheads, 700 nm light may also fall outside their ability for color discrimination. The variation in response of loggerhead hatchlings to 540, 560, and 580 nm light at varying intensity indicates that the xanthophobic response is not independent of light intensity.

Models of mechanisms by which sea turtles achieve a seaward orientation commonly employ the term brightness to denote the cue that guides hatchlings to the ocean (Verheijen and Wildschut, 1973; van Rhijn, 1979; Mrosovsky and Kingsmill, 1985). Unfortunately, brightness in this usage is not a currently measurable value. Brightness from the perspective of the sea turtle hatchling must certainly incorporate intensity in proportion to a species-specific action spectrum. Could perceived brightness, however, be influenced by other biased responses to color? Brightest-direction models must incorporate a definition for brightness that considers such complexities if those models are to explain the orientation behavior we observed in loggerhead and green turtle hatchlings.

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