Apéndice I
Medidas de Control para Evitar Contaminación por Luz en la Playa

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TECHNICAL REPORTS

Understanding, Assessing, and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches

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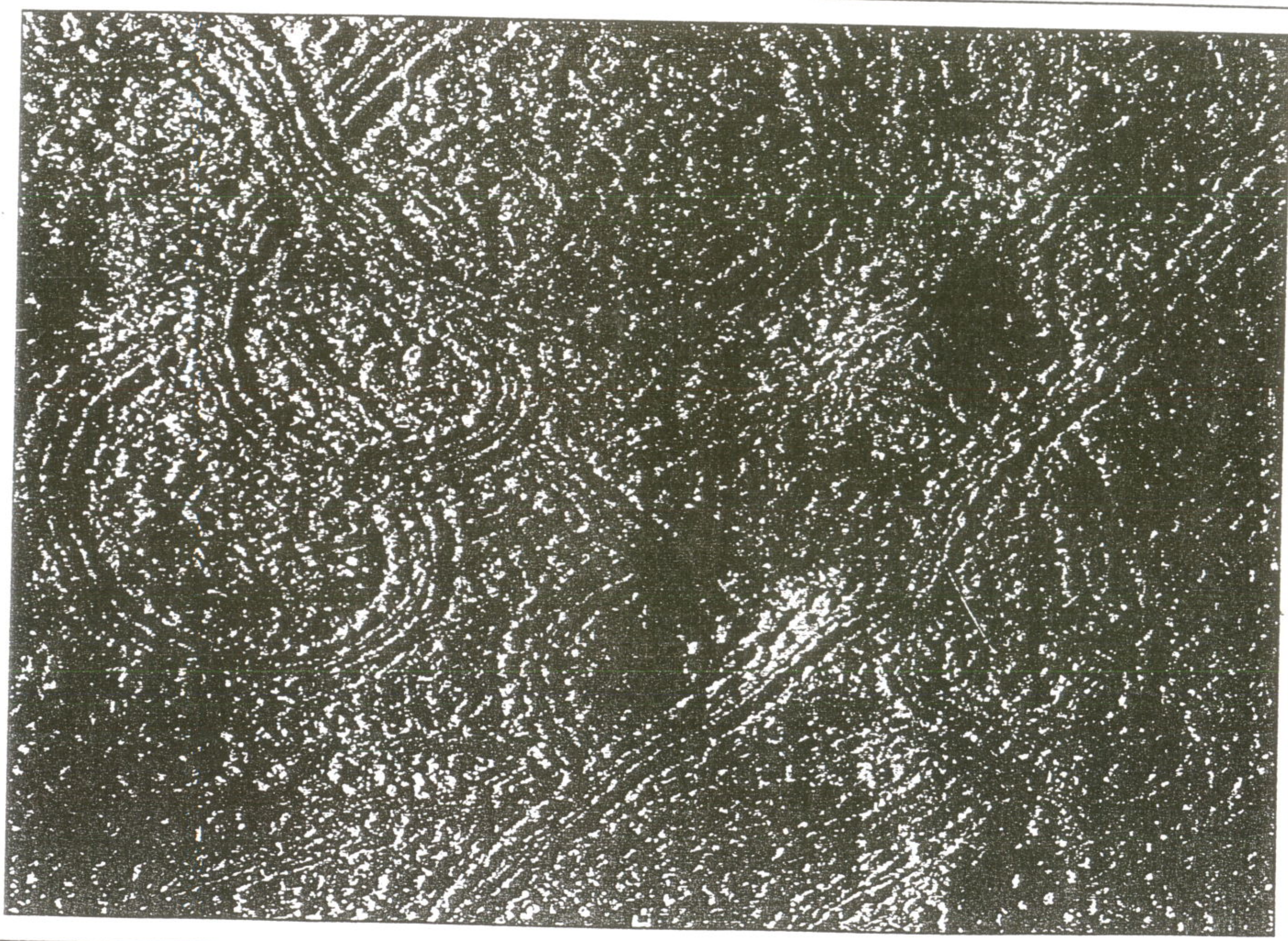

Florida Department of Environmental Protection

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Understanding, Assessing, and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches

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Cover Photograph

Tracks of disoriented loggerhead (*Caretta caretta*) hatchlings, Melbourne Beach, Florida. Photograph by Blair E. Witherington.

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Understanding, Assessing, and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches

Executive Summary

Sea turtle populations have suffered worldwide declines, and their recovery largely depends upon our managing the effects of expanding human populations. One of these effects is light pollution—the presence of detrimental artificial light in the environment. Of the many ecological disturbances caused by human beings, light pollution may be among the most manageable. Light pollution on nesting beaches is detrimental to sea turtles because it alters critical nocturnal behaviors, namely, how sea turtles choose nesting sites, how they return to the sea after nesting, and how hatchlings find the sea after emerging from their nests.

Both circumstantial observations and experimental evidence show that artificial lighting on beaches tends to deter sea turtles from emerging from the sea to nest. Because of this, effects from artificial lighting are not likely to be revealed by a ratio of nests to false crawls (tracks showing abandoned nesting attempts on the beach).

Although there is a tendency for turtles to prefer dark beaches, many do nest on lighted shores, but in doing so, the lives of their hatchlings are jeopardized. This threat comes from the way that artificial lighting disrupts a critical nocturnal behavior of hatchlings—crawling from their nest to the sea. On naturally lighted beaches, hatchlings escaping from nests show an immediate and well-directed orientation toward the water. This robust sea-finding behavior is innate and is guided by light cues that include brightness, shape, and in some species, color. On artificially lighted beaches, hatchlings become misdirected by light sources, leaving them unable to find the water and likely to incur high mortality from dehydration and predators. Hatchlings become misdirected because of their tendency to move in the brightest direction, especially when the brightness of one direction is overwhelmingly greater than the brightness of other directions, conditions that are commonly created by artificial light sources. Artificial lighting on beaches is strongly attractive to hatchlings and can cause hatchlings to move in the wrong direction (misorientation) as well as interfere with their ability to orient in a constant direction (disorientation).

Understanding how sea turtles interpret light cues to choose nesting sites and to locate the sea in a variably lighted world has helped conservationists develop ways to identify and minimize problems caused by light pollution. Part of this understanding is of the complexity of lighting conditions on nesting beaches and of the difficulty of measuring light pollution with instrumentation. Thankfully, accurately quantifying light pollution is not necessary to diagnose a potential problem. We offer this simple rule: if light from an artificial source is visible to a person standing anywhere on a beach, then that light is likely to cause problems for the sea turtles that nest there.

Because there is no single, measurable level of artificial brightness on nesting beaches that is acceptable for sea turtle conservation, the most effective conservation strategy is simply to use "best available technology" (BAT: a common strategy for reducing other forms of pollution by using the best of the pollution-reduction technologies available) to reduce effects from lighting as much as practicable. Best available technology includes many light-management options that have been used by lighting engineers for decades and others that are unique to protecting sea turtles. To protect sea turtles, light sources can simply be turned off or they can be minimized in number and wattage, repositioned behind structures, shielded, redirected, lowered, or recessed so that their light does not reach the beach. To ensure that lights are on only when needed, timers and motion-detector switches can be installed. Interior lighting can be reduced by moving lamps away from windows, drawing blinds after dark, and tinting windows. To protect sea turtles, artificial lighting need not be prohibited if it can be properly managed. Light is properly managed if it cannot be seen from the beach.

Best available technology also includes light

TRUST

The sea produced an ancient form
with aquatic wings for soaring
that gouged the sand away from tide
above the ocean's pouring.

She abandoned hope to trust the past,
heaved forth the future and at last,
buried it and left.

Now, two moons hence, little turtles pip,
with soft struggling bodies hatching.
The sands ensconce as eggs are ripped
by contorted masses scratching.

The siblings toil at a common chore
to whittle ceiling into floor,
until at sand's surface just short of sky,
the unsettled lie, becalmed.

The tangled turtles wait
as heat of day abates
and cool of night prods
their reluctance away.

At dusk the fits and starts begin
and then through claw and strain,
above their heads sand rains again,
and yields to sky of night.

This army boiling in the night gains might,
and in waves, pours forth to see the sight.
Soft flippers patter and wipe sand from view
that eyes might seize upon the cue that betrays the sea.

And then, eyes do, they catch the glow
and every hatchling keen
rushes on to the goal they know
but they have never seen.

As if clockwork toys tightly wound
they keep pace and bearing tight,
for unless the sea is quickly found,
they will not survive the night.

They choose their erring paths
with neither doubt nor anticipation,
and their consistency deals them life or death
with quiet resignation.

Thus, night wanes and sights of light remaining
scatter throngs persistent
and about the dune abundant obstacles restraining,
divide the dying from the spent.

Weakened few reach the sight they sought,
a deceptive brightness reassuring
where trusting forms are caught
by the sight of lights alluring.

Dawn now dries their searching eyes
and death now rests the weary.
Might fate have been more kind
to travelers more leery?

Were these turtles to awaken,
could they sense their mother's plight
having left her young forsaken
owing confidence in light?

Past's light offered not such bitter seas
nor played such deadly roles
to guide hatchlings on to sights like these
electric lights on poles.

Might we masters of the light adapt,
forgo complete control,
and lessen obsolescence
lest our presence take its toll?

To tread on earth with darkness soft
leaves not the night asunder
and preserves the stars and moon aloft,
and obsoleted wonders.

—BEW

Understanding, Assessing, and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches

Introduction

In the sliver of time since Europeans began migrating throughout the tropical oceans of the world, sea turtle populations have declined and many have been extirpated. As a group, sea turtles are considered dangerously close to extinction. Because of their precarious status, sea turtles have been afforded protection by local, state, provincial, and national laws and by international treaties. In the United States and its territories, the Endangered Species Act of 1973 prohibits all killing, harming, and harassment of six species of sea turtles: the green turtle *(Chelonia mydas)*, the loggerhead *(Caretta caretta)*, the hawksbill *(Eretmochelys imbricata)*, Kemp's ridley *(Lepidochelys kempi)*, the olive ridley *(Lepidochelys olivacea)*, and the leatherback *(Dermochelys coriacea)*.

It is perhaps on ocean beaches where the activities of people and sea turtles are most conspicuously intertwined. On these narrow strips of sand, people live, recreate, and conduct commerce—and sea turtles come to reproduce. Although sea turtles spend very little of their lives on beaches, their activities there are critical to the creation of the next generation. Sea turtles leave little more disturbance on the beach than a mound of sand and are likely to make no more of an impression on human inhabitants than to awaken a sense of wonder. Humans, however, can cause profound environmental changes in the places they visit. The consequences of such changes for sea turtles can be severe and are of great concern to those working for sea turtle conservation. An integral goal of sea turtle conservation efforts is to reduce deleterious human effects such as habitat alteration. In this manual, we will examine a distinctive and particularly damaging type of habitat alteration that affects sea turtles at the nesting beach, namely, light pollution—the introduction of artificially produced detrimental light into the environment.

Light from artificial sources differs markedly from other pollutants both in its form—light is energy rather than substance—and in its effect on sea turtles. Whereas heavy metal, petroleum, and other chemical pollutants produce predominately physical or physiological effects, the effect that light pollution has on sea turtles is essentially psychological. For sea turtles, artificial light is best described not as a toxic material but as misinformation. With its great potential to disrupt behaviors that rely on correct information, artificial lighting can have profound effects on sea turtle survival. Critical sea turtle behaviors affected by light pollution include the selection of nesting sites by adult turtles and the movement off the beach by hatchlings and adults.

Raymond (1984a) presented the first summary of the effects of light pollution on hatchling sea turtles and some potential solutions to this problem. The present manual can be considered an expanded update of the material presented by Raymond. Our goals here are to offer new perspectives on the problem of light pollution at sea turtle nesting beaches and to present recently acquired information both on the problem itself and on the strategies and mechanics by which the problem can be solved. Our presentation is geared for biologists, conservationists, and managers who may be consulted about or charged with solving problems caused by artificial lighting on sea turtle nesting beaches. However, this manual is also meant to inform the lay person who may work or live near a nesting beach and is concerned about sea turtle conservation.

Problems: The Effects of Artificial Lighting on Sea Turtles

Sea Turtle Nesting

THE NESTING PROCESS

Sea turtles are marine reptiles that deposit their eggs above the high-tide line on sand beaches. Sea turtle nesting is seasonal and for most populations begins in late spring and concludes in late summer. Although more than one sea turtle species may nest on the same beach, their nesting seasons are often slightly offset. In Florida (USA), for instance, leatherbacks begin nesting in mid-March and conclude in mid-July, loggerheads begin nesting in early May and conclude in late August, and green turtles begin nesting in early June and conclude by mid-September (Meylan *et al.*, 1995).

Except for the flatback turtle (*Natator depressus*; B. Prince, personal communication), Kemp's ridley (Pritchard and Marquez, 1973), and some populations of hawksbills (Brooke and Garnett, 1983), sea turtle nesting occurs almost exclusively at night. All sea turtle species have in common a series of stereotyped nesting behaviors (descriptions given by Carr and Ogren, 1959; Carr *et al.*, 1966; Bustard, 1972; Ehrenfeld, 1979; Hirth and Samson, 1987; Hailman and Elowson, 1992; Hays and Speakman, 1993), although there are subtle differences between species and some elements of this behavior may vary between individuals and between nesting attempts. For example, nesting behavior may vary in where turtles emerge onto land, in where on the beach they begin to construct their nests, in whether they abandon their nesting attempts and at what nesting stage they abandon the attempts, and in the directness of their paths as they return to the sea. These variations in nesting behavior can affect the success of egg deposition and hatchling production and can affect the well-being of the nesting turtle.

During the process of nesting, an adult female sea turtle 1) emerges from the surf zone, 2) crawls up the beach to a point typically between the high-tide line and the primary dune, 3) prepares the nest site by pushing or digging surface sand away to form a "body pit," 4) digs an "egg cavity" within the body pit using the rear flippers, 5) deposits eggs within the egg cavity, 6) covers the eggs with sand, 7) camouflages the nest site by casting sand, principally with front-flipper strokes, 8) turns toward the sea, and 9) crawls into the surf (Hailman and Elowson, 1992, include an additional "wandering" phase). For the most part, the pattern of each of these behaviors (how they are performed) is not affected as greatly by external stimuli (such as the presence of humans or lights) as are the "decisions" that determine the timing, duration, and accuracy of these behaviors. Functionally, these decisions affect the selection of a nest site, the abandonment or abbreviation of nesting behaviors, and the accuracy of sea-finding.

DISRUPTION OF NEST-SITE SELECTION

Sea turtles select a nest site by deciding where to emerge from the surf and where on the beach to put their eggs. The most clearly demonstrated effect of artificial lighting on nesting is to deter turtles from emerging from the water. Evidence for this has been given by Raymond (1984b), who reported on a dramatic reduction in nesting attempts by loggerheads at a brightly lighted beach site in Florida. Elsewhere in Florida, Mattison *et al.* (1993) showed that there were reductions in loggerhead nesting emergences where lighted piers and roadways were close to beaches. Mortimer (1982) described nesting green turtles at Ascension Island as shunning artificially lighted beaches. Additional authors have noted a relationship between lighted beach development and reduced sea turtle nesting: Worth and Smith (1976), Williams-Walls *et al.* (1983), Proffitt *et al.* (1986), and Martin *et al.* (1989) for loggerheads in Florida; Witherington (1986), Worth and Smith (1976), and Ehrhart (1979) for green turtles in Florida; and Dodd (1988), Witham (1982), and Coston-Clements and Hoss (1983) in reviews of human impacts on sea turtle nesting. Salmon *et al.* (1995a) found that loggerheads that do nest on beaches where the glow of urban lighting is visible behind the dune tend to prefer the darker areas where buildings are silhouetted against the artificial glow. Other authors have mentioned reduced nesting activity at lighted and developed beaches (Talbert *et al.*, 1980) or nesting in spite of lighted development (Mann, 1977) but have reserved judgment on the effects of lighting because of other contributing factors such as increased human activity near developed areas.

In addition to evidence pointing to a correlation between lighted beaches and reduced nesting, there is evidence from experimental field work that directly implicates artificial lighting in deterring sea turtles

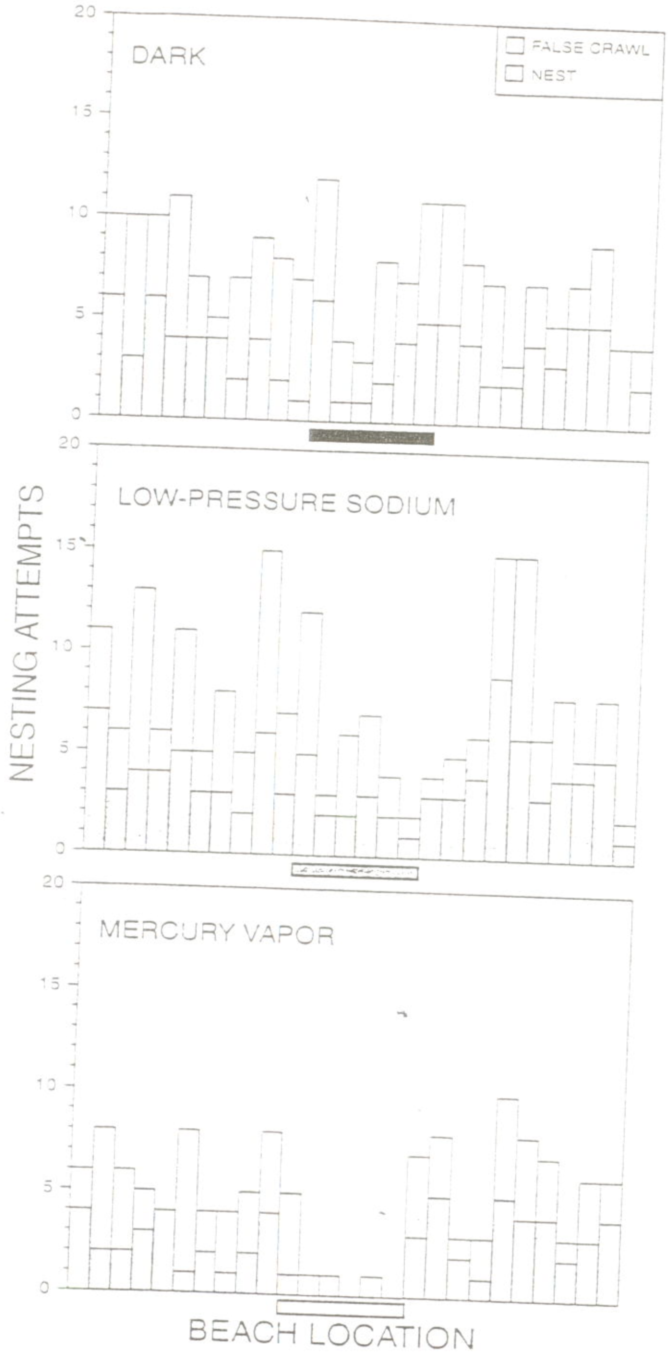

Figure 1. The distribution of loggerhead nesting attempts on a 1,300-m stretch of beach at Melbourne Beach, Florida. The beach locations were divided into 50-m sections. The horizontal bars show the section of beach where luminaires were set up—either lighted mercury-vapor luminaires (open bar), lighted low-pressure sodium-vapor luminaires (shaded bar), or luminaires that were not lighted (dark bars). Data are from Witherington (1992a).

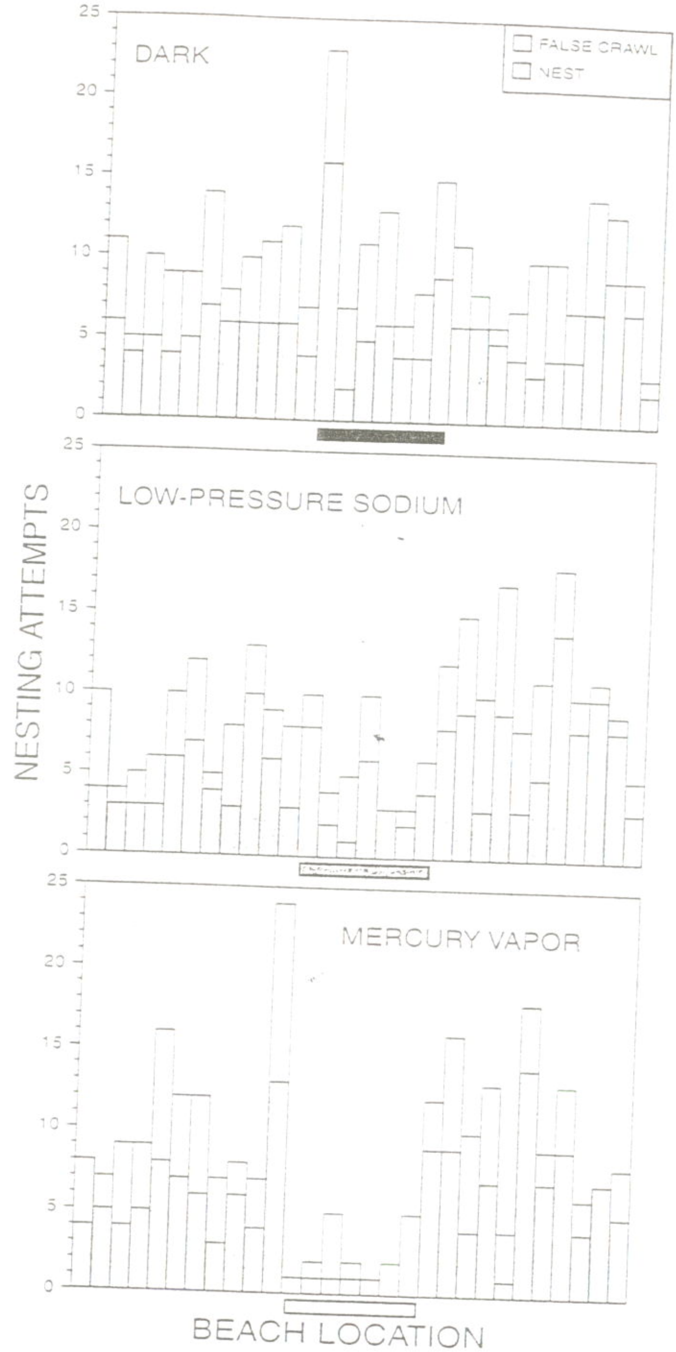

Figure 2. The distribution of green turtle nesting attempts on a 1,450-m stretch of beach at Tortuguero, Costa Rica. Identifications are as in Figure 1.

from nesting (Witherington, 1992a). In these experiments, undeveloped nesting beaches were left dark or were lighted with one of two types of commercial light sources. Both green turtles and loggerheads showed a significant tendency to avoid stretches of beach lighted with white mercury-vapor luminaires (Figures 1 and 2). However, any effect of yellow low-pressure sodium-vapor luminaires on loggerhead or green turtle nesting could not be detected. Because the mercury-vapor lighting reduced both nesting and nonnesting emergences, it seems that the principal effect of artificial lighting on nesting is to deter turtles from exiting the water. This means that one cannot rely on a ratio of nesting and nonnesting tracks to reveal effects from artificial lighting. The reason why artificial lighting deters nesting emergences is not known. It may be that artificial lighting on a beach is perceived by the turtles as daylight, which may suppress behavior that is usually nocturnal.

Once on the beach, sea turtles select a place to make a nest. In the field experiments by Witherington (1992a), artificial lighting had no effect on how far from the dune sea turtles placed their nests. Nest placement on the beach may depend most heavily on nonvisual cues such as temperature gradients (Stoneburner and Richardson, 1981).

The artificial lighting of sea turtle nesting beaches can be considered a form of habitat loss. When lighting deters sea turtles from nesting beaches, nesting turtles may be forced to select less appropriate nesting sites. Worth and Smith (1976) reported that loggerheads deterred from nesting re-emerged onto beaches outside their typical range. Murphy (1985) found that loggerheads that were repeatedly turned away as they made nesting attempts chose increasingly distant and inappropriate nesting sites in subsequent nesting attempts. If we assume that sea turtles choose nesting sites based upon favorable conditions for safe nesting and the production of fit offspring, then light pollution can be said to force some turtles into suboptimal nesting habitat. At suboptimal nesting beaches, the number of hatchlings produced and their survivorship may be compromised, and hatchling sex ratios may be affected. There is also the potential that turtles deterred from nesting may shed their eggs at sea. In the Caribbean, adult female turtles held in pens during the nesting season often drop their eggs without nesting (A. Meylan, personal communication).

NESTING BEHAVIOR ABANDONMENT AND ABBREVIATION

Sea turtles that emerge onto beaches often abandon their nesting attempts before putting their clutches of eggs into the sand. Nesting success (the number of nests divided by attempts) varies between beaches and between species. Among 28 Florida nesting beaches surveyed in 1994, nesting success for loggerheads was 53% (n = 52,275 nests), 52% for green turtles (n = 2,804 nests), and 83% for leatherbacks (n = 81 nests) (Florida Department of Environmental Protection, Index Nesting Beach Survey Program). Nesting success for Florida loggerheads in 1994 was 61% (n = 3,704 nests) at the undeveloped beaches of the Canaveral National Seashore and 45% (n = 6,026 nests) at the residential and heavily armored beaches of Jupiter Island. Sea turtles will abandon nesting attempts when they encounter digging impediments, large structures, unsatisfactory thermal cues, or human disturbance; when there are injuries to the rear flippers; or when other influences recognized thus far only by the turtles deter them (BEW and REM, unpublished data; Stoneburner and Richardson, 1981; Fangman and Rittmaster, 1993).

Sea turtles are most prone to human disturbance during the initial phases of nesting (emergence from the sea through egg-cavity excavation; Hirth and Samson, 1987), and during this period, green turtles are reported to be deterred by people with flashlights (Carr and Giovannoli, 1957; Carr and Ogren, 1960). Our experiences with nesting loggerheads and green turtles have been that the presence of people moving within the field of view of a turtle may cause abandonment just as often as—and perhaps more often than—hand-held lighting, but this has yet to be studied experimentally.

In one study (Witherington, 1992a), stationary lighting could not be shown to cause loggerheads and green turtles to abandon their nesting attempts on the beach. In that study, however, so few turtles emerged onto the mercury-vapor–lighted portion of the beach that recorded nesting attempts were insufficient for a proper test of nesting success.

Although sea turtles are less prone to abandon nesting attempts once oviposition has begun, the normal post-oviposition behavior of covering the eggs and camouflaging the nest site can be abbreviated if a turtle is disturbed. Johnson *et al.* (1996) measured the behavior of loggerhead turtles observed by turtle-watch ecotourism groups and found that the "watched" nesting turtles had shorter-than-average bouts of nest covering and camouflaging. We have made similar observations of turtles "watched" by unorganized groups of people with flashlights. In one instance, BEW observed that a green turtle illuminated by a bright flashlight covered its eggs, cast sand, and began a return to the sea in less than five minutes following oviposition (green turtles normally take approximately 50 minutes for these behaviors; Hirth and Samson, 1987). We know of no studies that attribute an abbreviation of nesting behavior to the effects of stationary lighting near nesting beaches.

DISRUPTION OF SEA-FINDING

After a sea turtle has camouflaged her nest, she must orient toward the sea and return there. Experiments with blindfolded green turtles that had finished nest-hatchlings are described as having an integrated array or "raster system" of light sensors within both eyes that would allow a hatchling to instantaneously interpret the brightest direction. Rather than sensing detail, this hypothesized raster system would integrate a measure of brightness over a broad area. This mechanism is referred to as a telotaxis system (Verheijen and Wildschut, 1973; Mrosovsky and Shettleworth, 1974; Mrosovsky *et al.*, 1979)—telotaxis (*telopos* = seen from afar, *tasso* = to arrange) refers to a fixation on and movement toward a target stimulus.

Unfortunately, the differences in these proposed mechanisms are too subtle to allow them to be separated by the experimental evidence at hand. The more "complex" a phototropotaxis mechanism becomes, the more it functionally resembles a telotaxis mechanism (Schöne, 1984). The actual visual-neural system that hatchlings use to turn toward the brightest direction and maintain that orientation may incorporate aspects of each of the proposed mechanisms.

A MODEL FOR MEASURING BRIGHTNESS

To determine the brightest direction, hatchlings must be able to "measure" brightness. Knowing the properties of the "brightness detector" used in this measurement is essential to our understanding a hatchling's response to its world. Although simplistic, modeling hatchlings as biological brightness-detectors is a useful way to introduce the properties of light that most affect hatchling orientation.

Spectral properties of the brightness detector.—The spectral properties of a detector—or an eye—reveal its sensitivity to different wavelengths of light. In bright light, we see different wavelengths and combinations of wavelengths as color. However, independent of color, some wavelengths appear brighter to us than others, just as there are some wavelengths we cannot see.

The term "brightness" is often used in the sea turtle orientation literature and generally refers to the intensity and wavelength(s) of light relative to the spectral sensitivity of an individual (Ehrenfeld and Carr, 1967; Mrosovsky, 1972; Rhijn, 1979; Mrosovsky and Kingsmill, 1985). Brightness is undoubtedly in the eye of the beholder. The different-colored photopigments and oil droplets within the retina of a sea turtle's eye (Granda and Haden, 1970; Liebman and Granda, 1971; Granda and Dvorak, 1977) provide a unique set of conditions that influence how sea turtles make their determination of brightness.

Researchers have learned much about sea turtles' perception of brightness by using a procedure

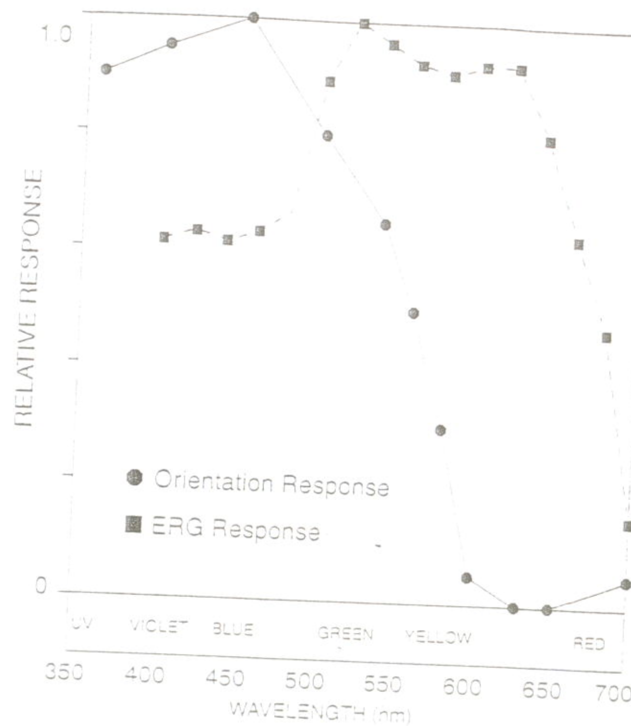

Figure 4. A comparison of the orientation and physiological (ERG) responses of green turtle hatchlings to colored light. The orientation response curve shows how attractive the light is to green turtle hatchlings, and the ERG response curve gives an approximation of how bright the light appears to them. Orientation data are from Witherington (1992b), and ERG data are adapted from Granda and O'Shea (1972). Figure adapted from Witherington (in press); used with permission.

called electroretinography (ERG) to measure the relative electrical potential across retinas of turtles exposed to different wavelengths of light. ERG data show that green turtles are most sensitive to light in the violet to orange region of the visible spectrum, from 400 to 640 nm (Figure 4; Granda and O'Shea, 1972). In daylight, green turtles show a greater spectral sensitivity within the shorter-wavelength (blue) region of the spectrum than humans do.

Although ERG data provide important physiological information, the most direct way to determine the effects of spectral light on orientation is to conduct behavioral experiments. The earliest studies on hatchlings' responses to light wavelength employed broad-band (multiple-wavelength–transmission) filters to vary the wavelengths that reached orienting hatchlings (Mrosovsky and Carr, 1967; Mrosovsky and Shettleworth, 1968). Although reactions to specific wavelengths could not be determined, it was clear that the green turtle hatchlings studied were more attracted to blue light than to red light.

In later experiments, researchers used narrow-

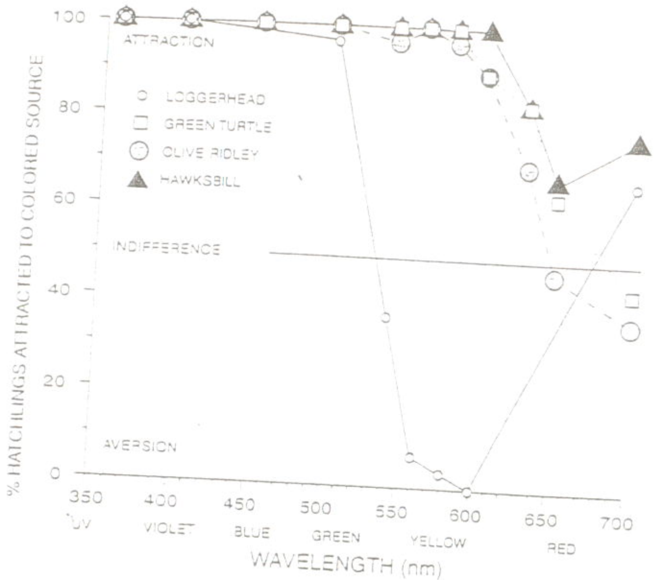

Figure 5. *Orientation responses of four species of sea turtle hatchlings to colored light sources. Responses were measured as the proportion of hatchlings that chose a window lighted with a colored light source over a similar but darkened window (Witherington, 1992b). The loggerhead differed from the other species in that it showed an aversion to light in the yellow region of the spectrum. Figure adapted from Witherington (in press) and Lohmann* et al. *(in press); used with permission.*

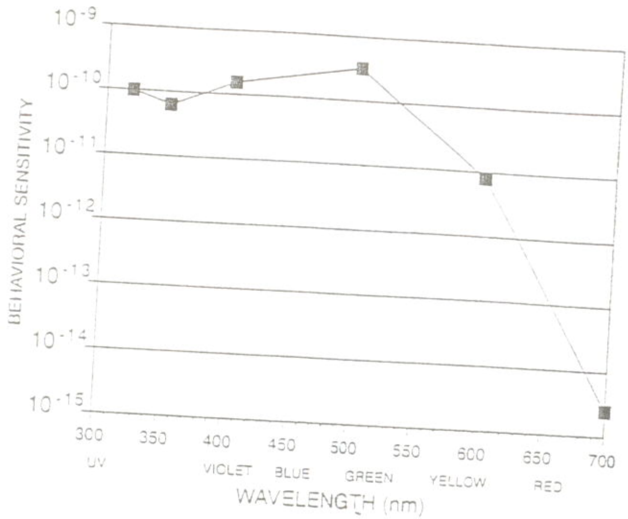

Figure 6. *Behavioral sensitivity of loggerhead hatchlings to low-intensity colored light, represented as the inverse of the light-source radiance required to evoke significantly directed orientation in groups of hatchlings (n = 30 per wavelength). At the low light levels represented here (approximately the radiance of the sky on a full-moon night, and dimmer), there was orientation toward the light source at all wavelengths. The ordinate is a log scale of the units (photons/s/m²/sr)⁻¹. Data are from Witherington (1992b). Figure adapted from Witherington (in press) and Lohmann* et al. *(in press); used with permission.*

band (monochromatic) filters to vary the wavelengths reaching loggerhead, green turtle, hawksbill, and olive ridley hatchlings (Witherington and Bjorndal, 1991a; Witherington, 1992b). The use of monochromatic filters allowed a simple measure of light intensity so that researchers could determine the responses of hatchlings to a set number of photons at each of several wavelengths. As in previous experiments, hatchlings showed a preference for short-wavelength light. Green turtles, hawksbills, and olive ridleys were most strongly attracted to light in the near-ultraviolet to yellow region of the spectrum and were weakly attracted or indifferent to orange and red light (Figure 5). Loggerheads were most strongly attracted to light in the near-ultraviolet to green region and showed an unexpected response to light in the yellow region of the spectrum. At intensities of yellow light comparable to a full moon or a dawn sky, loggerhead hatchlings showed an aversion response to yellow light sources (Figure 5), but at low, nighttime intensities, loggerheads were weakly attracted to yellow light (Figure 6). It may be that the hatchlings cannot discriminate color at low light levels. This is common for animals (such as turtles) that have rod-and-cone retinas (Granda and Dvorak, 1977).

It should come as no surprise that humans and sea turtle hatchlings see the world differently. For most of their lives, sea turtles see the world through a blue ocean filter (water selectively absorbs reddish, long-wavelength light), so it makes sense that sea turtles would be most sensitive to short-wavelength light.

Because sea turtle hatchlings respond to light that we cannot see (ultraviolet light) and are only weakly sensitive to light that we see well (red light), instruments that quantify light from a human perspective (such as most light meters) cannot accurately gauge brightness from the perspective of a sea turtle. Humans also cannot assess color exactly as a sea turtle would. Although we can see colors, we cannot tell what assortment of wavelengths may make up those colors. For example, a light source emitting both 525-nm (green) and 645-nm (red) light, a source highly attractive to hatchlings, appears to a human observer to emit yellow light comparable to a 588-nm monochromatic source, which would be only weakly attractive to hatchlings (Rossotti, 1983).

Directional properties of the brightness detector.—Just as a hatchling's detector has a sensitivity to specific light wavelengths, it is also sensitive to light direction. The directional properties of a detector determine how much of the world the detector measures

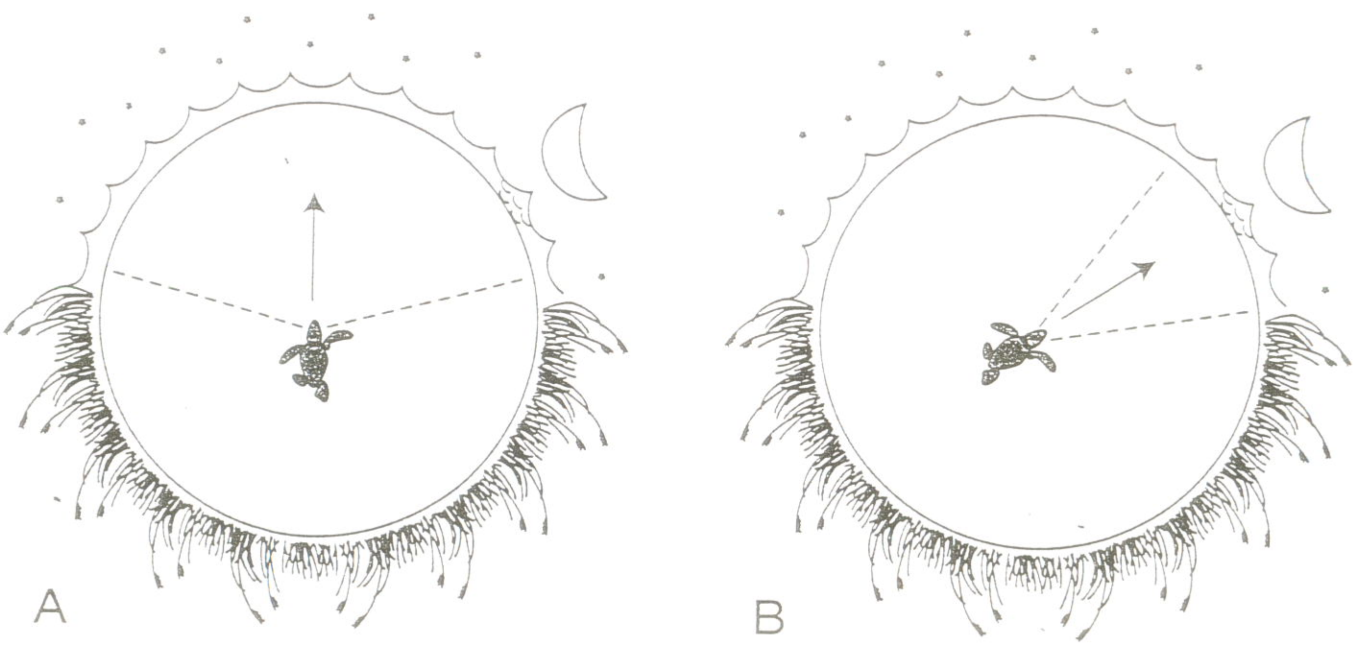

Figure 7. The consequences of measuring the brightest direction with a wide (A) or a narrow (B) angle of acceptance. Hatchlings A and B both orient toward the center of the brightest portion of the horizon within their angle of acceptance (shown by dotted lines). Hatchling B's path to the water would be considerably longer. Figure adapted from Witherington (in press); used with permission.

at any one instant. These properties are described by a specific "cone of acceptance" or by bidimensional (horizontal and vertical) "angles of acceptance." The height and breadth of a detector's acceptance cone critically influences brightness measurements and the determination of brightest direction (Figure 7). This conceptual acceptance cone may be only a portion of a turtle's complete field of view.

The horizontal component of the acceptance cone for green turtle and olive ridley hatchlings (Verheijen and Wildschut, 1973) and for loggerhead hatchlings (Witherington, 1992b) has been deduced from the way that hatchlings orient in controlled light fields. In these studies, light fields were artificially controlled so that detectors with different acceptance-cone widths measured different brightest directions. Hatchlings of each species typically oriented in the brightest direction as it would be measured with a wide acceptance cone, approximately 180° horizontally.

To determine the vertical component of the acceptance cone, the researchers cited above measured the orientation of hatchlings presented light sources that were positioned at various vertical angles. The angular height of this vertical component was approximated to be "a few degrees" for green turtles and olive ridleys (Verheijen and Wildschut, 1973) and between 10° below and 30° above the horizon for loggerheads (Salmon and Wyneken, 1990; Witherington, 1992b). Although the measures are approximate, it is clear that light closest to the horizon plays the greatest role in determining orientation direction.

The detector model for hatchling orientation predicts that hatchlings measure brightest direction by integrating the light they detect over a broad and flat acceptance cone (Figure 8). Again, we see that the attributes of this hypothetical detector differ from those of most light meters. The most commonly found light meters, illuminance meters, measure light with an acceptance cone that is less flattened and not as wide as the acceptance cone that hatchlings use. Another type of light meter, a luminance or "spot" meter, measures light with a very narrow acceptance cone. Careful consideration should be given to the directional attributes of a light-measuring instrument if its measurements are to be used in predicting hatchling behavior.

COLOR CUES

In addition to brightness cues, color may also influence the direction that a hatchling orients. Color discrimination (the ability to identify colored light) is different from spectral sensitivity. An animal may be able to detect many light wavelengths that it cannot tell apart. The fact that sea turtles have cones in their retinas is not sufficient evidence that sea turtles see color; however, some behavioral evidence can be

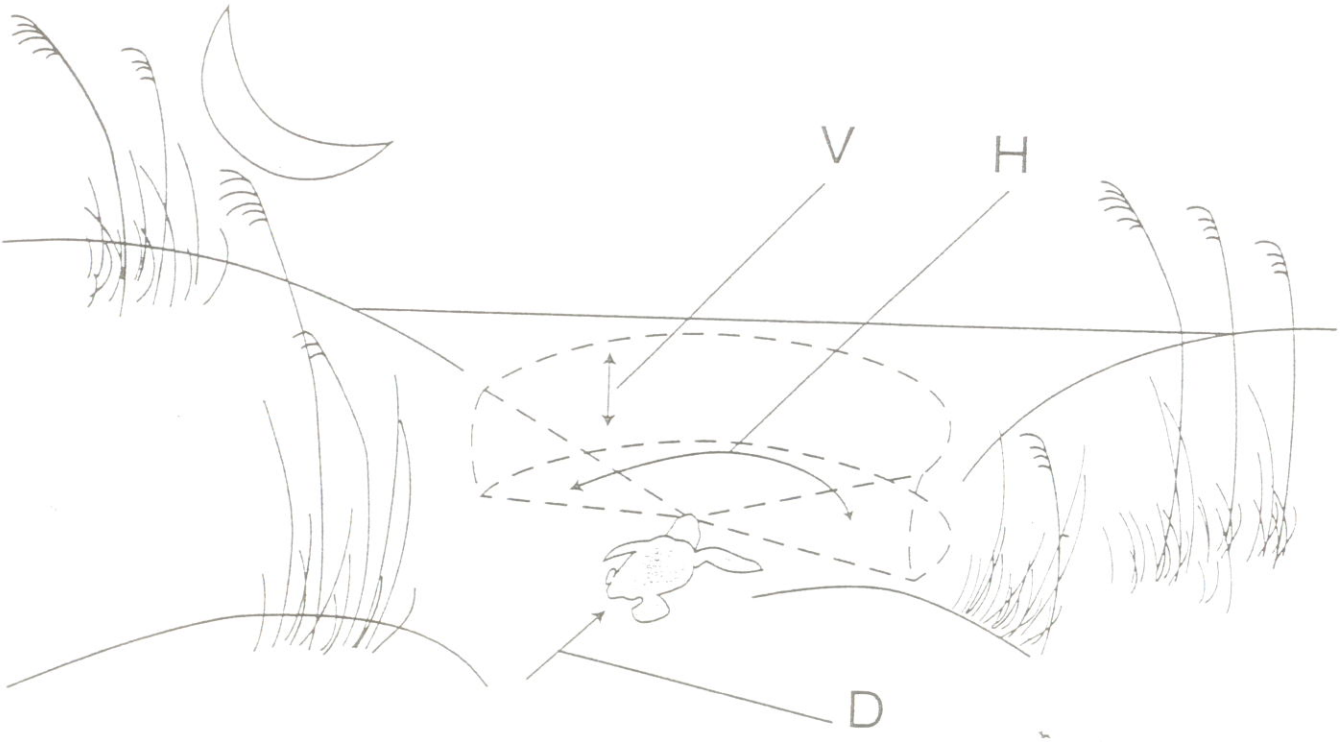

Figure 8. *A hypothetical cone of acceptance that describes how a sea turtle hatchling measures the brightest direction. Light within this cone of acceptance is integrated into an assessment of brightness for the direction D. The vertical component of the cone (V) is approximately 10°–30° from the horizon, and the horizontal component of the cone (H) is approximately 180°. This description is based on data from studies of green turtles, olive ridleys, and loggerheads (Verheijen and Wildschut, 1973; Witherington, 1992b). Figure adapted from Witherington (in press); used with permission.*

convincing. Currently, there is some behavioral evidence that sea turtles can see color and that color may play some limited role in sea-finding.

In one of the first published discussions of sea-finding cues in hatchlings, Hooker (1911) suggested that the blue of the ocean itself may provide an attraction. The evidence used to test this hypothesis should be weighed carefully. Green turtle hatchlings do tend to prefer directions illuminated with blue light over directions illuminated with red light (Mrosovsky, 1972), but is this truly a color choice? Do hatchlings prefer the color blue, or are they simply selecting the brightest direction as determined by a detector that is most sensitive to blue wavelengths? The answer may be that both are true.

Conditioning experiments have shown that loggerheads do have some ability to discriminate among colors (Fehring, 1972). Whether loggerheads can and do use this ability in sea-finding, however, can best be determined by comparing the wavelengths a hatchling can detect best (as might be measured with ERG) with the wavelengths a hatchling prefers in orientation experiments. ERG data for the green turtle show that red light must be approximately 100 times more intense than blue light for the two colors to elicit a similar magnitude of response at the retina (Granda and O'Shea, 1972). Yet in a series of behavioral experiments using broad-band colors, Mrosovsky (1972) found that red light had to be approximately 600 times more intense than blue light in order for green turtle hatchlings to show an equal preference for the two colors. Such a bias against long-wavelength light was also demonstrated by behavioral studies in which monochromatic light was used (Figure 4; Witherington and Bjorndal, 1991a). In this study, the greatest disparity between ERG response and color preference was found in the yellow-orange region of the spectrum, near 600 nm. Although it is apparent that green turtles see yellow light well, light of this color is relatively unattractive to orienting hatchlings.

Although no ERG data currently exist for the loggerhead, the way that loggerhead hatchlings behave toward some colored light sources indicates that they too may use color cues in sea-finding. The aversion to yellow light, or xanthophobia, that loggerhead hatchlings show sets them apart from other sea turtle species. Loggerhead hatchlings are weakly attracted to low-intensity yellow light sources but show an aversion to higher-intensity yellow light. Similar increases in the light intensity of near-ultraviolet, violet, and green light sources do not elicit a change in response from attraction to aversion, which indicates that the aversion to yellow light is related to color rather than brightness. Additional experiments with loggerheads have shown an interesting relationship between attraction to short-wavelength light and aversion to yellow light: the two responses appear to be additive. In evidence of this, Witherington (1992b) showed that adding high-intensity yellow light to an otherwise attractive light source (thereby making the light source brighter) will decrease its attractiveness to loggerhead hatchlings.

There is no empirical evidence to suggest why both loggerhead and green turtle hatchlings show little or no attraction to sources that are rich in yellow light. One hypothesis is that by reducing their attraction to yellow-rich light sources, hatchlings can avoid being misdirected by the sun or the moon. Because the rising or setting sun or moon lies within a hatchling's vertically flat acceptance cone, these celestial sources have the potential to affect hatchling orientation to some degree. However, a universal characteristic of celestial light sources is that they become yellower and redder when they are near the horizon (a sunset appears yellowish red because the blue light from the sun at dusk is attenuated by the thickness of the atmosphere that the light must pass through to reach an observer). Actually, some controversy exists as to whether the rising sun does affect sea-finding in hatchlings. Whereas Parker (1922), Ehrenfeld and Carr (1967), and Rhijn (1979) reported that loggerheads, green turtles, and hawksbill turtles are affected insignificantly by the sun on the horizon, Mrosovsky (1970), Mrosovsky and Kingsmill (1985), and Witherington (1992b) reported that loggerhead, green, and hawksbill turtles are affected. By all accounts, given its brightness, the effects of the sun on hatchling orientation seem small.

SHAPE CUES

Many authors have suggested that the patterns of light and shadow associated with visible shapes help sea turtle hatchlings find the sea. On beaches, hatchlings tend to orient toward "open areas" and "open horizons" and away from "silhouetted horizons," "dune profile," and "vegetation" (Hooker, 1911; Parker, 1922; Mrosovsky and Shettleworth, 1968; Limpus, 1971; Salmon *et al.*, 1992, 1995b).

Hatchling sea turtles' response to shape cues has been studied less extensively than their response to brightness has. To be sure, there is some debate as to how well hatchlings on a beach can discriminate shape. Based upon the optical characteristics of a sea turtle's eye, one would expect them to see most clearly in sea water and to be relatively myopic on land (Ehrenfeld and Koch, 1967). But because hatchling eyes are small and their depth-of-focus is large, hatchlings may be able to distinguish shape well (Northmore and Granda, 1982). The most recent evidence from laboratory studies suggests that sea turtle eyes may be able to distinguish shape well enough to resolve individual stars in the sky (Northmore and Granda, 1991).

Both Limpus (1971) and Salmon *et al.* (1992) have presented convincing evidence that loggerhead and green turtle hatchlings tend to orient away from silhouettes. On most beaches this tendency would direct hatchlings away from the profile of the dune and toward the ocean. But do hatchlings respond to the shape of the dune itself or to the way the dune influences the brightest direction? By their nature, dune silhouettes darken the horizon and would be expected to influence brightest direction as hatchlings measure it. Although some effects of shape and silhouette may be independent of brightness, isolating these effects is not a straightforward process. In fact, our confidence in distinguishing shape-cue orientation from brightness-cue orientation should be only as great as our confidence in our ability to measure brightness as hatchlings do.

Determining the specific roles of shape and brightness in hatchling orientation has been attempted in cue-conflict studies. In these studies, both green turtle (Rhijn and Gorkom, 1983) and loggerhead (Witherington, 1992b, c) hatchlings tended to orient away from sets of alternating black and white stripes and toward a uniformly illuminated direction, even when the striped direction was brightest. Orientation away from a horizon that has spatial patterns of light and shadow (*i.e.*, shapes) could assist sea-finding by directing hatchlings away from the structure associated with the dune (*e.g.*, vegetation) and toward the comparatively flat and featureless ocean. However, the demonstration that hatchlings can orient with respect to shape cues does not necessarily mean that hatchlings require them for sea-finding.

The necessity of shape cues for sea-finding has been studied by depriving hatchlings of form vision (*i.e.*, the ability to discern shape). Mrosovsky and Kingsmill (1985) disrupted the form vision of loggerhead hatchlings by fitting them with waxpaper goggles and concluded that because the animals still oriented seaward, shape was not a primary cue in sea-finding. In a similar test, Witherington (1992b) placed loggerhead hatchlings within transparent cylinders that were covered with either waxpaper or nothing at all. These hatchlings were observed as they attempted sea-finding under what might be considered "challenging" conditions—at moonset on an east-facing beach. Under these conditions, hatchlings with a clear view of their surroundings oriented seaward, whereas hatchlings having their form vision disrupted by waxpaper oriented in the general direction of the setting moon.

OTHER LIGHT CUES

In addition to intensity, wavelength, shape, and direction, light can also vary in time (have a certain periodicity) and in both space and time (display motion) and can have a unique composition of polarized light. Motion has not yet been explored as a potential sea-finding cue. Periodicity has been examined and has been found to have some influence on hatchling orientation, but only as it relates to a brightness measure. Evidence for this comes from a study in which green turtle hatchlings preferred a constant light source over a flashing one only when the off-time of the flashing source was very long (Mrosovsky, 1978). This implies that hatchlings may integrate their measures of brightness over time.

Because water tends to polarize the light reflected from it, richness of polarized light has the potential to indicate the ocean direction. However, the experiments in which hatchlings viewed their world through waxpaper but maintained a seaward orientation showed that hatchlings depend little, if at all, on polarity cues (Mrosovsky and Kingsmill, 1985). Waxpaper, in addition to obliterating form, would have also depolarized the light that hatchlings saw. Additional laboratory evidence shows that at least among loggerhead hatchlings, there is no orientation preference between sources that are polarized or unpolarized or that have different directions of polarity (e-vector direction; Witherington, 1992b).

WHEN CUES CONFLICT

Brightness cues, shape cues, and color cues (under high-illumination only) all provide information to orienting sea turtle hatchlings. Because a hatchling's environment is complex and variable, having a compound set of cues to guide even the simplest of tasks makes sense. Any single cue by itself could, under some conditions, be misleading. But do conflicting cues present a real problem in nature, and if so, how do hatchlings balance the information from these cues in order to make a correct orientation decision?

In nature, cues do conflict. Brightness measurements made on nesting beaches where hatchlings orient to the sea show that the seaward direction is often brightest, but sometimes it is not (Rhijn, 1979; Wibbles, 1984; Witherington, 1992b). Measurements made under various conditions show that although the ocean is brightest on clear, moonless nights, the direction of the moon is brightest near moonrise and moonset (Witherington, 1992b).

Although it is not completely clear how hatchlings balance the information from conflicting orientation cues, experimental evidence indicates that this balance may be based upon the comparative strengths of the cues. In the cue-conflict experiments discussed earlier, influences of both brightest direction and shape were seen in some cases (Witherington, 1992b). Hatchlings tended to orient away from contrasting stripes even when the striped direction was twice the brightness of the uniformly lighted direction. But, when the striped direction was made three times brighter than the opposing direction, hatchling orientation became undirected, and when the striped direction was five times brighter, most hatchlings oriented toward the stripes. It seems then that orientation either away from contrasting shapes, irrespective of brightest direction, or toward the brightest direction, irrespective of contrasting shapes, depends on how strong the brightest direction happens to be. This strength of the brightest direction is known as "directivity." As the directivity of the light field a hatchling sees increases, the brightest direction becomes more pronounced, less ambiguous perhaps, and seemingly a greater orientation stimulus.

Are shape cues more important than brightness cues to orienting hatchlings? To answer this question, researchers will need to measure and compare the strengths of the two types of cues. At present, there is no common unit of measurement that can be used in making a comparison. For now, we can say that both shape cues and brightness cues are important for correct seaward orientation in a variably lighted world.

DISRUPTION OF SEA–FINDING

OBSERVATIONS OF SEA–FINDING DISRUPTION

Accounts of sea-finding disruption presented in the literature do not properly represent the vast extent of the problem. Only the most conspicuous cases are observed and reported, such as when hatchlings have been crushed on roadways (McFarlane, 1963; Philibosian, 1976; Peters and Verhoeven, 1994; REM and BEW, personal observations), burned to death in the flames of an abandoned fire (Mortimer, 1979), or led onto the playing field of a baseball game in progress (Philibosian, 1976). More often than not,