Chapter 13

The problem of photopollution for sea turtles and other nocturnal animals

BLAIR E. WITHERINGTON

Notice: This material may be protected by copyright law (Title 17 U.S. Code).

One of the most conspicuous ways we alter the natural world is to light the darkness. To an observer in space looking down at the night-time half of the Earth, a patchwork glow of artificial lighting reveals the extent of our presence on the planet. Beyond providing a space-age index of human habitation, this errant light is known to have its own unique and profound ecological effects. These effects have the potential to create fundamental shifts in the selective pressures on living organisms and should be of keen interest to conservation biologists.

Verheijen (1985) used the term 'photopollution' to describe the introduction of detrimental artificial light into the environment. To be sure, light is not among the more familiar pollutants. Unlike most other pollutants, light is energy rather than substance and the measurement of its biological effects must account for varying sensitivities (among animals and instrumentation) to light's many properties (intensity, wavelength, directivity, polarity, form, periodicity). The most important peculiarity of light as a pollutant is in its effects upon animals, the most harmful of which are upon behavioral systems, such as those controlling visual orientation and the timing of periodic behavior. In either case, 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 survival.

In the following discussion I present examples showing the consequences of behaviors disrupted by photopollution, offer mechanisms by which this disruption may occur, and list a number of strategies with which to address this conservation problem. A focus of this discussion is upon disrupted visual orientation, and in particular, the well-studied example of the effects of artificial lighting on the orientation of hatchling sea turtles. The research of lighting problems for sea turtles and the

pursuit of solutions to these problems can provide a model to shape similar conservation efforts for other species.

Examples

Disruption of visual orientation

Night-flying insects are commonly seen circling and colliding with point sources of light and are perhaps the best known organisms to have their orientation disrupted by artificial lighting (Schacht & Witt 1986). Workers studying insect phenology capitalize on this phenomenon to capture insects *en masse* in light-traps (Takahashi & Haruta 1986; Wada *et al.* 1987; Pedgley & Yathom 1993). Commercially available light-traps sold for pest-control ('bug zappers') are engineered to attract large numbers of insects and kill them with electricity (Syms & Goodman 1987). Insects die in great numbers at other light sources; however, their mortality is generally only reported as a concern when the density of dead insects interferes with the functioning of light sources or is otherwise a nuisance (Ali *et al.* 1994). Although the loss of insects to artificial lighting can be extensive, the ecological implications of this mortality are unknown.

The aggregation of fish and squid at artificial light sources has been discussed primarily as a phenomenon that assists harvesting (Ben-Yami 1976). Although the principal harm of artificial lighting for fishes may be to simply facilitate over-exploitation, the use of light in fisheries also may have some potential to conserve resources. Because fishes have species-specific responses to light intensity and color, light may be used to reduce the catch of non-target species in net fisheries that are otherwise indiscriminate (Clarke *et al.* 1986).

Sea turtles are affected profoundly by artificial lighting, making photopollution at sea turtle nesting beaches an important conservation issue for the six sea turtle species (of seven extant species) listed as threatened or endangered. Lighting deters sea turtles from emerging from the sea to nest on otherwise preferred beaches (Witherington 1992*a*). Where nesting on lighted beaches does occur, hatchlings emerging nocturnally from nests are unable to locate the sea and wander inland toward light sources. This sea-finding disruption (often termed disorientation) results in high hatchling mortality. Conspicuous examples include cases where hatchlings have been lured onto roadways and crushed (McFarlane 1963; Philibosian 1976; Peters & Verhoeven 1994) or burned to death in the

flames of an abandoned fire (Mortimer 1979). More commonly, however, 'lost' hatchlings are depredated by beach crabs or birds or become exhausted and dehydrated deep in dune vegetation. This mortality is most often inconspicuous, as in an example from Melbourne Beach, Florida, USA, where hundreds of dead Loggerhead (*Caretta caretta*) hatchlings were discovered beneath a single mercury vapor luminaire (L. M. Ehrhart, personal communication). At this site, the number of hatchlings and their varied conditions indicated that the light had attracted hatchlings for many nights. The dead hatchlings were only discovered after a close inspection of the grounds near the light source. In Florida each year, approximately one million hatchling sea turtles are misdirected by lighting which results in hundreds of thousands of hatchling deaths.

Mortality of nocturnally migrating birds at artificial light sources is well documented, and accounts show that many species are affected. The most acute bird-kills occur during periods when the moon provides little light or when cloud cover is heavy (Verheijen 1981). Literature accounts of specific bird-kill events show that the light sources responsible are varied. Examples include an oil-industry flare in northwestern Alberta, Canada, that killed approximately 3000 passerines representing 24 species during a period of a few days (Bjorge 1987). On a single night, flood lights at a park on Padre Island, Texas, USA, killed approximately 10 000 birds representing 39 species (James 1956). On a lighted boat off Alaska, approximately 6000 Crested auklets (*Aethia cristatella*) collided with the vessel nearly sinking it (Dick & Donaldson 1978). Lighthouses (Verheijen 1981), lighted towers (Kemper *et al.* 1966), airport ceilometers (Howell *et al.* 1954), and area lighting (James 1956; Reed *et al.* 1985) also mark areas where heavy bird mortality is known to occur. It is estimated that lighted television towers kill roughly a million migrating birds each year (Aldrich *et al.* 1966).

In endangered Hawaiian populations of petrels and shearwaters, fledgling birds leaving burrows in mountain nesting colonies fly toward the lighting of nearby resorts and are killed as they strike poles and buildings. This attraction to lighting is known to occur in 21 species of procellariiform birds (Reed *et al.* 1985).

Disruption of rhythmic behaviors

The natural periodicity of light intensity, both the differentiation of day and night and the change of day length with season, is critical to the timely

expression of many behaviors. One effect of artificial light sources is to alter the environmental periodicity on which rhythmic behaviors depend. Thus, migrations may occur during an improper season, reproductive behavior and territoriality in individuals may occur out of phase with the rest of the population, and behaviors selected for during the day are expressed at night.

There is ample laboratory evidence for the change of rhythmic behavior under artificial lighting conditions. Artificial light-periodicity has been shown to affect behaviors as diverse as the timing of death feigning in domestic chicks (Stahlbaum *et al.* 1986), emergence of wasps from pupae (Dahiya *et al.* 1993), reproductive swarming of polychaetes (Fong 1993), and the accuracy of the sun compass used by orienting birds (Foa & Saviozzi 1990).

Although the effects on captive animals are well documented, few field studies have been initiated to examine the light-periodicity effects on wild populations. There are some anecdotal observations. At street lighting, normally diurnal birds are known to call at night, and in lighted harbors marine polychaetes are sometimes seen to swarm outside the normal new-moon period. There are likely to be additional important but less conspicuous effects, yet it is presently unknown how widespread these phenomena may be.

Does photopollution matter?

Abundance and life history traits of animals in a population will determine whether it can withstand a specific level of additional mortality. For instance, many insects may appear to be locally or seasonally abundant and to have a high reproductive potential that would offset additional mortality. In such a simple population model, photopollution-related mortality would have to be high relative to population size for there to be a significant effect on population growth or decline. Yet, for many insect species the phenomenon of local or seasonal abundance is critical for reproduction. High mortality during these critical periods of abundance would have large effects on population stability, selection of behaviors, and therefore, the expression of aggregation phenomena. As aggregation phenomena diminish, predators that depend on insect aggregations would suffer in turn.

Additional ecological effects may ensue as artificial lighting affects insects that occupy specific niches, such as pollinators of night-flowering plants. Again, important effects are not only limited to reductions in

insect abundance but also include evolutionarily abrupt changes in the insect behavior patterns on which other organisms may depend. The ecological consequences of insect mortality at artificial light sources have yet to be adequately measured.

Compared with insects, there would seem to be a greater potential for photopollution-related mortality to cause population declines in turtles and birds. A population model for the Hawaiian dark-rumped petrel (*Pterodroma phaeopygia*) has shown that fledgling mortality caused by lighting near nesting colonies is an important factor in predicting whether the population is eventually extirpated (Simons 1984). For many sea turtle and bird populations, historic declines may be readily demonstrated, but underlying life history traits are poorly understood. Even without complete demographic information, however, it stands to reason that any level of mortality related to photopollution can be significant to a population that is threatened with extinction.

Artificial light sources and orientation systems

The best studied evidence of the effects of photopollution comes from animals that have trouble with visual orientation tasks near artificial light sources. In understanding this effect, it is important to understand the fundamental differences between light from artificial sources and light from celestial sources.

Clearly, it is celestial light rather than artificial light that has had the greatest opportunity to shape the evolution of visual orientation systems; but how does artificial light differ? Much of the answer lies in the nature of the light fields produced by the two kinds of sources. A light field is produced by a light source (or sources) but is measured from the perspective of an observer. It is a directional picture of all the light that can be detected by an observer. Light fields for celestial sources are only moderately directed, which means that although there may be one brightest direction, this direction is not tremendously brighter than other competing directions. These 'natural' light fields are moderated because both the observer and the illuminated features that the observer can see are similarly distant from the light source. Celestial light has a distant origin and reaches an observer not only directly but also indirectly as it is scattered in the atmosphere and reflected from the features on the Earth's surface (other competing directions). As a result, a celestial light field has clearly visible brightness from many directions.

Artificial light fields are produced by sources that are less intense than

celestial sources, although artificial sources appear bright to an observer due to their proximity. Other illuminated features that would contribute to an artificial light field (sky, clouds, landscapes) are distant relative to the proximity of the source, and the light reflected from them, comparatively dim. Consequently, an observer near an artificial light source experiences a highly directed light field that is overwhelmingly dominated by the light source.

Verheijen (1958) cited the high directivity of artificial light fields as the reason why artificial lighting elicits an abnormal 'light-trapping' response in many animals. He reasoned that as an orienting animal approaches an artificial source, the light field the animal perceives becomes less multidirectional (more directed) until a point is reached where the light source may be the only visible feature of the animal's world. At this point the animal would only be able to orient relative to this single feature in its environment.

An artificial source need not functionally blind an animal in order to disrupt its orientation: it need only disrupt the balance of visual information that an animal perceives. Proper spatial orientation is critical, especially to animals that migrate. Insects, amphipods, lobsters, fish, turtles, and birds all accomplish orientation by using multiple sensory modalities. As specific sensory cues fail or become contradictory, additional or 'backup' modalities assist in maintaining proper orientation (Schöne 1984). In such multimodal systems, sensory input is often weighted so that the relative intensity of a cue determines its influence on orientation. An animal near an artificial light source experiences high light intensity, and may be compelled to orient toward the light (use positive phototaxis) although this orientation may be counter to information from other directional cues.

The behaviors of animals affected by photopollution should not be thought of as so abnormal as to have no relation to behaviors that have been shaped by selection. Light cues are important to visually orienting animals, so it is reasonable to assume that before an animal is close enough to a light source to be overwhelmed by it, the animal may be using that light to guide (or in actuality, misguide) a visual orientation task that is critical for survival. Hatchling sea turtles are an example of this. When placed beneath a lighted luminaire on a beach at night, Loggerhead, Green turtle (*Chelonia mydas*), Hawksbill (*Eretmochelys imbricata*), and Olive ridley (*Lepidochelys olivacea*) hatchlings circle and appear unable to orient in a constant direction. When only 10 to 20 m away from the light source, however, hatchlings crawl on a constant bearing toward the light

source. This positive phototaxis is just as directed and deliberate as the orientation of hatchlings toward the sea on a naturally lighted beach. Hatchlings also show movement toward artificial light sources that are hidden from view, where light fields are not as directed as those produced by visible sources. I have often observed Loggerhead hatchlings crawling directly toward a wall of a beachfront building that is lit with a hidden floodlight. Although phototaxis alone would seem to explain this effect, there are additional mechanisms shaped by selection that influence the behavior of hatchlings near lighting. As I will discuss later, hatchlings do not always move in the brightest direction and can rely on additional visual information to lead them seaward.

In addition to positive phototaxis, many animals may be drawn to artificial light sources as a result of using them as reference cues in light-compass orientation systems. Bees, moths, and many bird species can maintain critical course bearings by using the sun, moon, an individual bright star, or star groups as reference points (Schöne 1984; Baker 1987). An animal that selects an artificial light source as a reference point for its light compass might not be able to maintain a constant orientation. To keep a straight course, an animal using a light compass keeps the bearing to a light-reference at a constant angle with the course bearing it has selected. When an earth-bound, artificial source is used as a light-reference, the deviation between the initial course bearing and the light-reference bearing will change with the position of the animal and defeat the function of the light compass. For example, a bird or insect may select an artificial light source to indicate a reference bearing at azimuth 45° (right of center). Initially, the animal's path may be relatively straight but as its flight takes it closer to the artificial source, it will begin to arc to the right toward the source until a point is reached when the animal actually circles the light source. From the animal's perspective, the light source will remain at a 45° angle to its path throughout the flight. Close to the light source, the animal may collide with the source or become light-trapped by high light-field directivity. Aircraft warning lights on tall towers would appear to be above the horizon to a flying bird and may deceptively mimic celestial point sources. This may explain high bird mortalities at these structures.

Searching for solutions

An understanding of species-specific visual orientation systems or light-mediated rhythmic behavior is fundamental to the correct application of

specific remedies to photopollution problems. One common-sense remedy, however, would seem to be universal: turn off the lights; but which lights? It may be that only some at a site contribute to the photopollution hazard. Extinguishing lights indiscriminately may not gather much support from property owners; therefore, a more prudent conservation strategy would be to selectively manage the light rather than prohibit it.

For a light management program to be guided successfully, certain questions should be answered. For instance, how important is light to the behavior in question? How much of a given light source is too much? Is there a compromise that will allow light required for human activity yet minimize light that can disrupt orientation? Is there a differential between the properties of light required for human use and the properties of light that can disrupt animal behaviors? Can disruption of orientation be minimized by introducing other cues that may guide multimodal systems? Where and when is light management needed (where and when do critical behaviors take place)?

Below I describe studies on hatchling sea turtle orientation that have begun to provide answers to these questions and that have resulted in some novel solutions to photopollution problems at sea turtle nesting beaches. Many solutions, however, are not novel and come instead from light management practices meant to solve problems that directly affect humans (e.g., energy efficiency, aesthetics, astronomical observation). As might be the case for other animals, sea turtle conservation has benefited from this synthesis of basic biological understanding and practical field techniques.

Light and hatchling sea turtle orientation

Like other animals affected by photopollution, sea turtles rely on accurate visual orientation to accomplish critical nocturnal tasks. For sea turtle hatchlings this critical task is the expeditious movement from nest to sea (sea-finding). Even moderate delay of sea-finding can be deadly for hatchlings.

Photopollution also has been shown to deter nesting and thus limit the extent of nesting habitat for sea turtles (Witherington 1992*a*). However, lighting that is bright enough to disrupt sea-finding in hatchlings often is not bright enough to deter females from nesting. Hatchling mortality from lighting is a significant conservation problem because nests are commonly placed on beaches that are too bright to allow hatchlings to escape.

Sea turtle hatchlings emerge from their sand nests almost exclusively at night (Witherington *et al.* 1990) and, under natural lighting conditions, move immediately and directly from nest to sea (Fig. 13.1). The inability of hatchlings to orient seaward when wearing bilateral blindfolds or when their view of the ocean is blocked by light shields or dune topography indicates that the principal ocean-recognition cues are visual (Mrosovsky & Shettleworth 1968, 1975; Mrosovsky 1972). Although hatchling sea turtles can respond to some non-visual cues, specifically beach slope (Rhijn 1979; Salmon *et al.* 1992), these cues appear to have a minor influence on directional movement even when visual cues are not present.

Hatchlings show a strong tendency to orient toward the brightest direction in a way that is predicted well by a complex phototropotaxis model (Mrosovsky & Kingsmill 1985). In this model, hatchlings turn to balance the visual input of multiple comparators at the retina of each eye

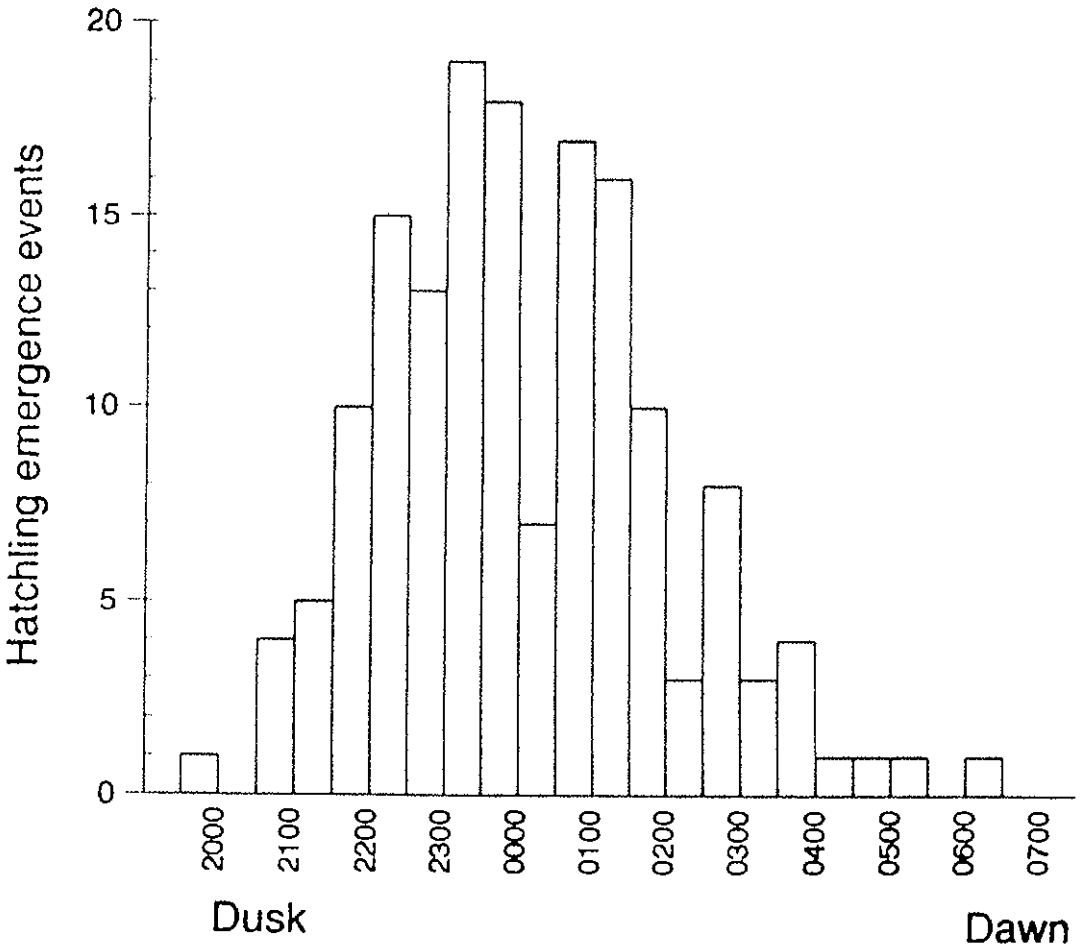

Fig. 13.1. Timing of 157 Loggerhead hatchling emergence events from natural nests on a Florida beach between 29 July and 1 September 1988. An emergence event was defined as the movement of ten or more hatchlings from nest to sea. Data from Witherington *et al.* (1990).

so that the hatchling is oriented toward the brightest horizon. Such a mechanism is thought to facilitate sea-finding by orienting hatchlings toward the horizon with the greatest portion of visible sky.

To assess lighting that may disrupt sea-finding, it is important to understand the criteria with which hatchlings 'measure' brightness. Some understanding of the spectral properties of this measure has been gained through determinations of relative electrical potential across retinas exposed to spectral light (electroretinography, ERG). The ERG spectrum for the dark-adapted Green turtle shows that the animal's eye is

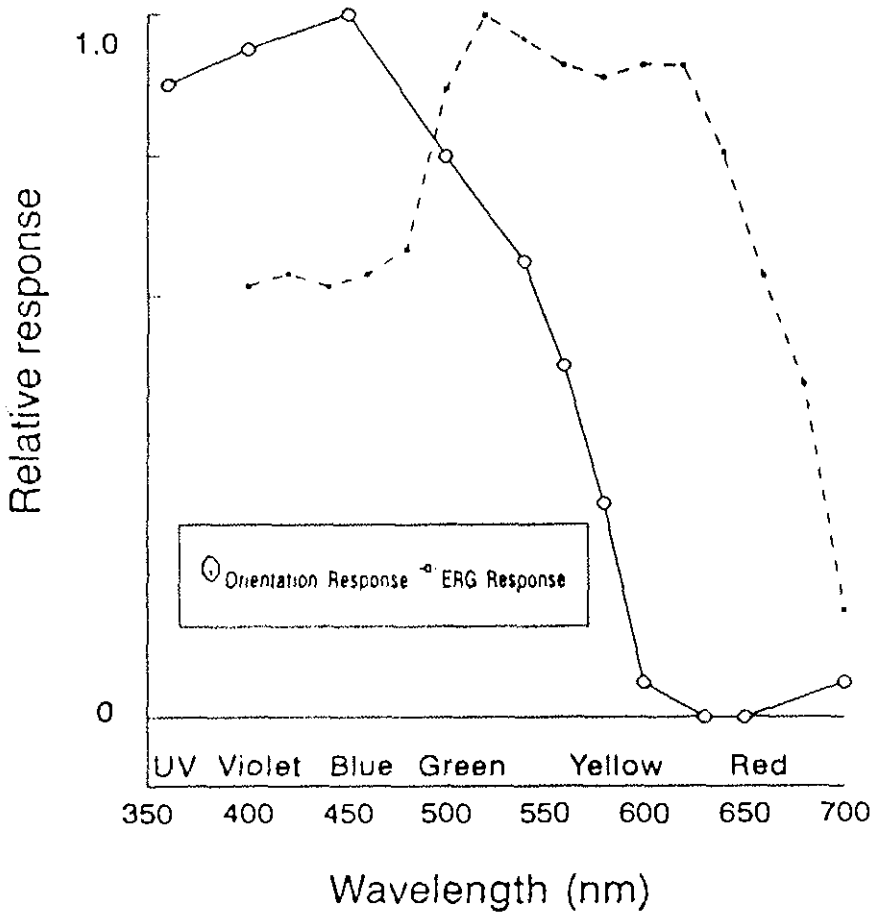

Fig. 13.2. Physiological and behavioral responses to spectral light in dark-adapted Green turtle hatchlings. The behavioral response curve represents the proportion of green turtle hatchlings in a modified Y-maze choosing a window lighted with colored light at the wavelengths indicated. The opposing window was lighted with an unvarying source (Witherington 1992*b*). Although wavelength at the colored-light window varied, radiance remained at 1.44×10^{17} photons s^{-1} m^{-2} nm^{-1} (approximate radiance of a full-moon night sky). The electroretinography (ERG) response curve is adapted from Granda & O'Shea (1972) and represents log sensitivity among wavelengths. Absolute intensity of the ERG light source was reported to be 2.7×10^{17} photons s^{-1} m^{-2} at 580 nm.

most sensitive in the blue-green to orange region of the visible spectrum, from 500 to 640 nm (Fig. 13.2; Granda & O'Shea 1972).

In addition to measuring what spectral light animals can see, it is important to measure how they respond behaviorally to spectral light. To measure the influence of spectral light on orientation behavior, Witherington & Bjorndal (1991*a*) conducted a series of two-choice light-preference experiments. Using a modified Y-maze, we measured hatchling attraction to high-intensity (greater than the illuminance of a full-moon night sky) diffuse light of various wavelengths presented relative to a second source of constant intensity and color (peak emission at 520 nm). Wavelengths that Green turtle hatchlings were most likely to orient toward did not coincide with their peak ERG sensitivity (Fig. 13.2). Although Green turtles can see yellow light comparatively well, they are only weakly attracted to yellow sources.

Among the four species of sea turtle hatchlings tested, there are two distinct patterns of spectral light preference (Fig. 13.3; Witherington 1992*b*). When dark-adapted Green turtle, Hawksbill, and Olive ridley hatchlings are presented high-intensity, diffuse spectral light and the option to orient toward or away from the source, hatchlings show attraction to short-wavelength light (ultraviolet-yellow) and are indifferent to long-wavelength light (red; Fig. 13.3). In contrast, Loggerhead hatchlings are attracted to ultraviolet-green light, are indifferent to green-yellow and red light, and move away from yellow light. In additional trials with Loggerhead hatchlings, neither blue-green nor red light prompted the aversion response seen for yellow light even when intensities were up to 100 times the intensity of yellow light. This suggests that the aversion to yellow may involve color perception rather than a response to brightness mediated by spectral sensitivity.

The Loggerhead's unique aversion to yellow light and the Green turtle's apparent discounting of yellow light occur only at what are probably photopic light levels (intensity sufficient for cone vision). To measure loggerheads' orientation responses to low-intensity spectral light, I conducted an orientation titration (Witherington 1992*b*). The apparatus was an enclosed circular arena with 72 pitfalls at the perimeter and a single light window in the perimeter wall. In this titration, light intensity of a given wavelength at the window was increased incrementally with each of several hatchling groups released at the arena center, until a hatchling group showed statistically directed orientation. At these low, threshold light-levels, all orientation was toward the light source for all wavelengths, including yellow. As in experiments with higher-

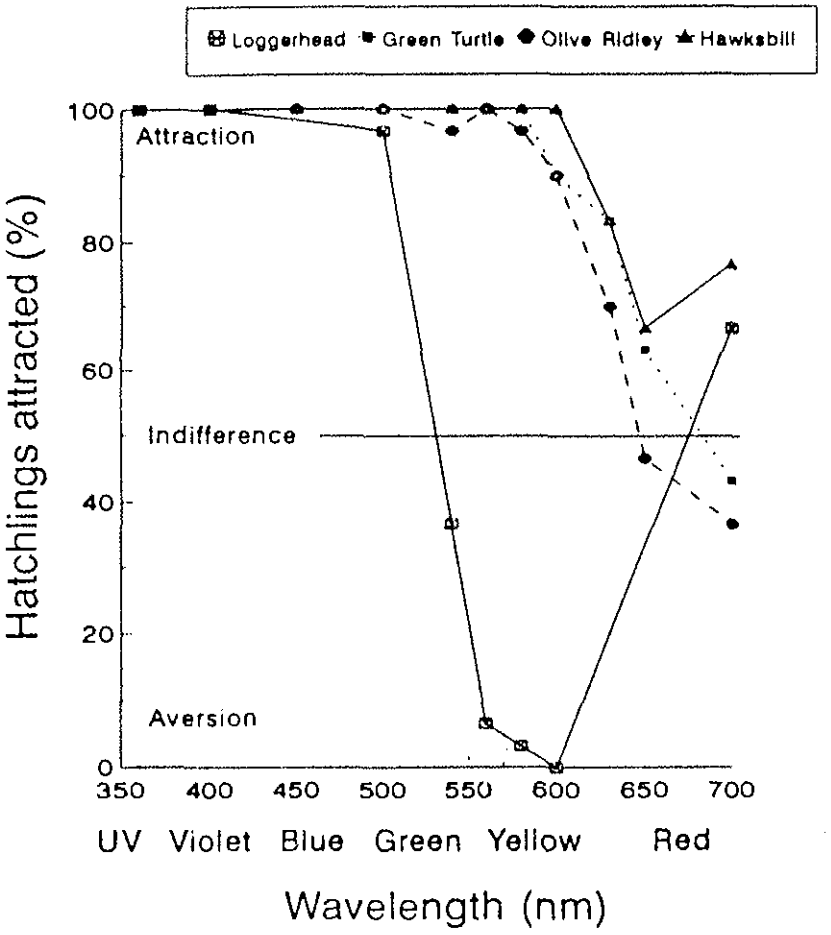

Fig. 13.3. Orientation responses to colored light from hatchlings from four species of sea turtles. Responses were measured as the proportion of hatchlings in a modified Y-maze choosing a window lighted with colored light at the wavelengths indicated. The opposing window was not lighted (Witherington, 1992*b*). Radiance of the lighted window remained at 1.44×10^{17} photons s^{-1} m^{-2} nm^{-1}. Aversion indicates that hatchlings predominately chose the dark window over the lighted window.

intensity light, ultraviolet-green light was most attractive (i.e., required the lowest intensity to elicit directed orientation; Fig. 13.4). Threshold intensities of yellow and red light were approximately one and five orders of magnitude higher than the threshold intensities for the shorter wavelengths studied. Loss of color perception with scotopic vision (night vision depending upon rod photoreceptors) may explain the lack of yellow aversion at these low light levels. It is at these low light levels that sea turtle hatchlings most often must locate the sea.

In addition to the weighing of spectral information, hatchlings also factor the relative direction of light into their measure of brightness. Sensitivity to directional light in hatchlings can be characterized by a specific 'cone of acceptance,' which describes how much of the world a

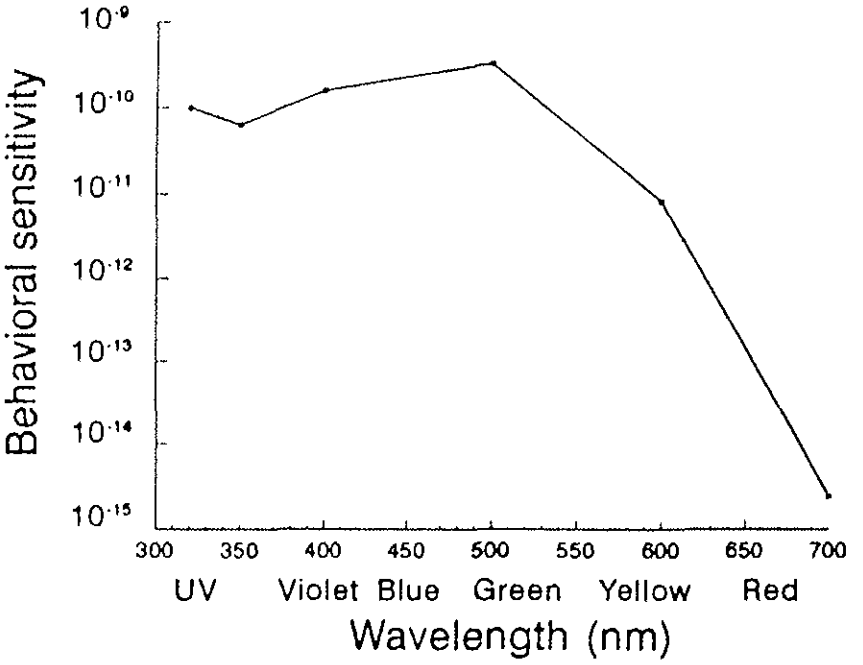

Fig. 13.4. Behavioral sensitivity of loggerhead hatchlings to low-intensity spectral light. Behavioral sensitivity is represented as the inverse of the light-source radiance required to evoke directed orientation in groups of individually released hatchlings ($n=30$ per group). Orientation at light thresholds was toward the light source. The ordinate is a log scale of the units (photons s^{-1} m^{-2} nm^{-1} $sr)^{-1}$. Data are from Witherington (1992*b*).

hatchling measures at any one instant (Fig. 13.5). An acceptance cone encompasses the angular span over which a brightness measurement is integrated and may be different from the turtle's field of view. The height and breadth of a hatchling's (or light detector's) acceptance cone critically influence its assessment of brightest direction and can determine whether point sources or a broad glow will have the greatest influence on measured brightness.

The horizontal component of the acceptance cone for Green turtle, Olive ridley, and Loggerhead hatchlings has been deduced through studies of hatchling orientation in controlled light fields (Verheijen & Wildschut 1973; Witherington 1992*b*). In these studies, hatchlings oriented within a vertically striped cylinder having many 'brightest directions' that varied according to width of the acceptance cone. On average, hatchlings of each species chose directions that corresponded with the brightest direction as measured with a wide acceptance cone (approximately 180° horizontally) (Fig. 13.5). To determine the vertical component of the hatchling's acceptance cone, researchers observed orientation in hatchlings that were presented light sources at varying vertical angles.

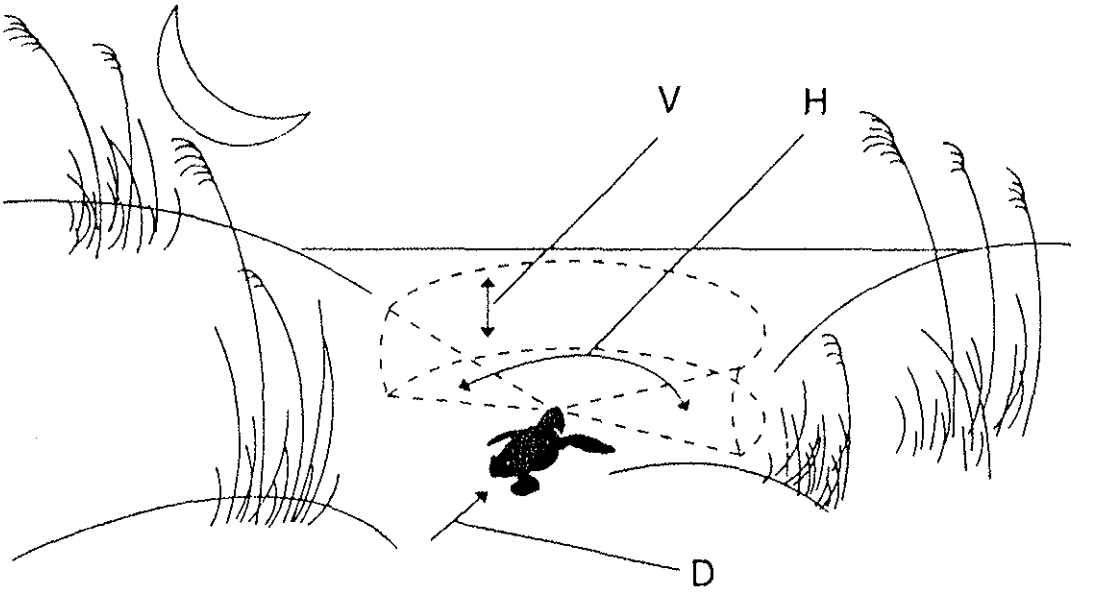

Fig. 13.5. Hypothetical cone of acceptance for the assessment of brightest direction by a sea turtle hatchling. The vertical component of the cone (*V*) is approximately 10° to 30° from the horizontal plane. The horizontal component of the cone (*H*) is approximately 180°. Light sources within this cone of acceptance are thought to be integrated into a measure of brightness for the direction D.

The vertical component of the acceptance cone was found to be a small span (approximately 30° or less) and centered near the horizon (Verheijen & Wildschut 1973; Salmon *et al.* 1992; Witherington 1992*b*). This vertically flat acceptance cone indicates that light closest to the horizon plays the greatest role in determining orientation direction. The horizontal breadth of the acceptance cone means that irradiance (light reaching the hatchling) is a better measure of relevant brightness than radiance (light emanating from a source). Integrating light measurement over a broad range may be important in mitigating the effects of the sun and moon on orientation direction (Fig. 13.6).

Although the brightest direction has an important influence on hatchling sea-finding orientation, hatchlings also respond to shape cues. Both Limpus (1971) and Salmon *et al.* (1992) have presented convincing evidence that Loggerhead and Green turtle hatchlings tend to orient away from darkened silhouettes. On most beaches this tendency would direct hatchlings away from the profile of the dune and toward the ocean. However, this response could be an epiphenomenon that results from brightest-direction orientation. Dune silhouettes by their nature darken the portion of the horizon within a hatchling's cone of acceptance in addition to presenting a characteristic shape.

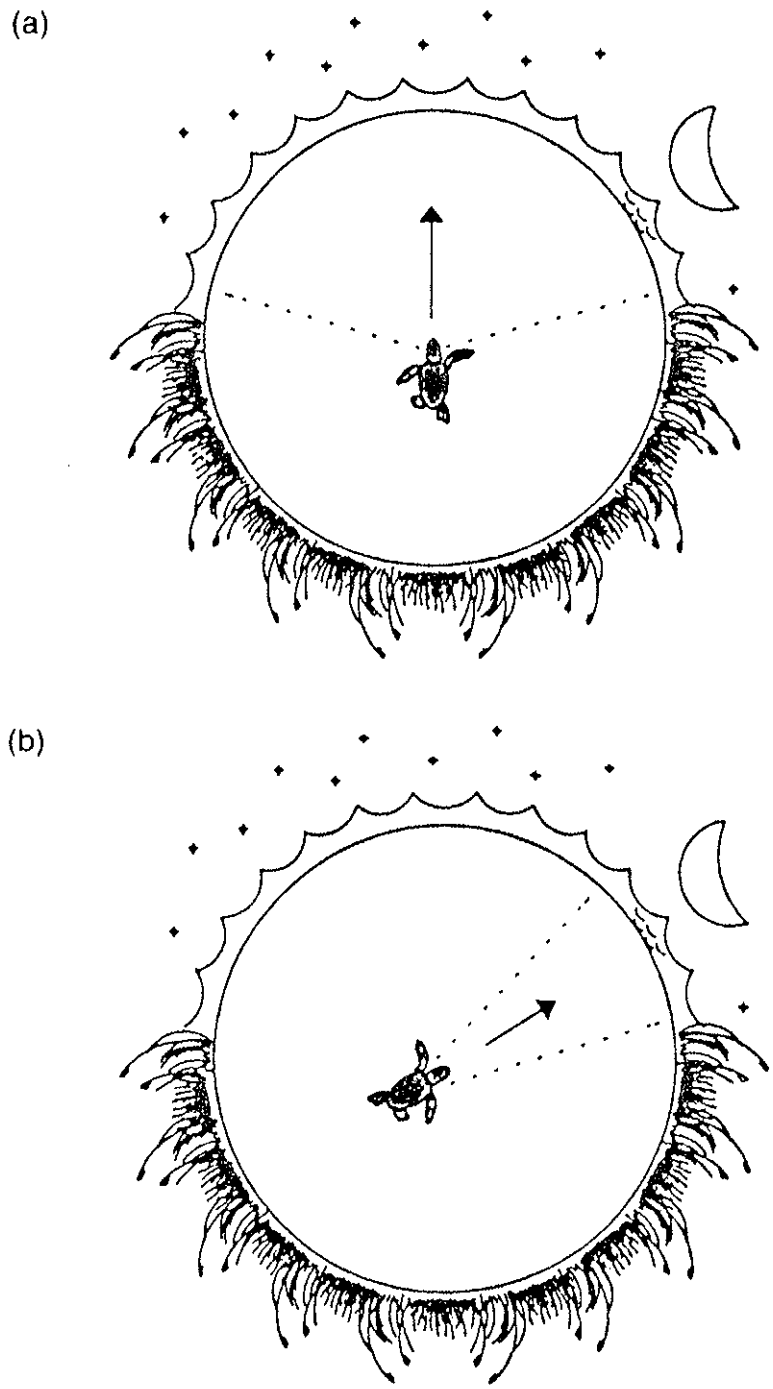

Fig. 13.6. Orientation consequences of brightness assessments using two hypothetical angles of acceptance. Hatchlings (a) and (b) both orient toward the center of the brightest horizon as measured within their respective angles of acceptance (dotted lines). Hatchling (a) uses a broad angle of acceptance and has the most accurate seaward orientation. Hatchling (b), having a narrow angle of acceptance, is directed toward the rising moon.

Elucidating the effects of shape on orientation, independent of the effects of brightness, is not a straightforward task. One's confidence in distinguishing shape-cue orientation from brightness-cue orientation should only be as great as one's confidence in measuring brightness as hatchlings do. Although our understanding of a hatchling's response to brightness remains at a basic level, there are clear indications that shape does influence orientation direction.

The effects of shape and brightness on hatchling orientation have been studied in cue-conflict experiments in which brightness was measured with instruments having the broad, flat acceptance cone described above. Both Green turtle and Loggerhead hatchlings tend to orient away from sets of vertical black and white stripes and toward an opposing, uniformly illuminated direction (open horizon) in the laboratory (Rhijn & Gorkom 1983; Witherington 1992*b*). In Loggerhead hatchlings, orientation away from contrasting stripes persists even when the striped direction is approximately twice the brightness of the open horizon (Witherington 1992*b*). When the striped horizon is brightened to three times the brightness of the open horizon, however, orientation of groups of hatchlings is randomly directed, and only after the striped horizon is made approximately five times brighter do hatchlings significantly orient in that direction.

In Loggerhead hatchlings, orientation, either away from contrasting shapes irrespective of brightest direction or toward the brightest direction irrespective of contrasting shapes, depends upon the directivity of the light field from the perspective of the hatchling. As this directivity increases, the brightest direction becomes more pronounced, less ambiguous perhaps, and apparently a greater orientation stimulus to the hatchling. An aversion to portions of the horizon that have visible structure (i.e., shapes as opposed to openness, variable spatial patterns of light as opposed to a uniform pattern) would benefit sea-finding. Commonly, nesting beaches have a vegetated dune that provides a structured profile in contrast with a flat and featureless ocean.

In nature and under artificial conditions, cues do conflict. Brightness measurements (with the spectral and directional considerations outlined above) made on nesting beaches indicate that the brightest direction is often not seaward (Rhijn 1979; Witherington 1992*b*). Measurements made under varying natural conditions show that the brightest direction depends largely on the direction of the moon during moonset and moonrise (Witherington 1992*b*). Under natural lighting conditions, regardless of the brightest direction, released hatchlings orient to the sea.

Measured light fields are most directed when artificial lighting is present, and on these lighted beaches, hatchlings are most likely to orient in the brightest direction, toward lighting (generally inland).

By presenting an unambiguous brightest direction to hatchlings, artificial lighting may be perceived as a supernormal sea. At such high levels of light directivity, brightness cues may be weighted so that shape cues are essentially ignored. Although hatchlings possess a multimodal visual orientation system that directs seaward movement under a variety of natural conditions, the function of this system is defeated in the presence of artificial lighting.

Lessons from sea turtles in understanding photopollution

From studies of hatchling orientation come a number of observations that may be common to other animals affected by photopollution.

(1) Although ERG spectral curves can be used to approximate the sensitivity of a behavior to spectral light, the most direct way to determine this is to measure the spectral sensitivity of the behavior itself. In doing so, one should measure the behavior where and when the behavior is normally expressed (such as the measurement of seafinding in hatchlings taken directly from the nest at night).

(2) Changing the spectral properties of an artificial light source can be an important way to reduce the effect it has on animal behavior. In some sea turtles, there is a reduced sensitivity to yellow and red light.

(3) Spectral sensitivity of a behavior and the extent to which a behavior is disrupted may be closely tied to light intensity. Behavioral experiments should be conducted at more than one light intensity level.

(4) Just as an animal may have a specific spectral sensitivity to light, it also may have a specific directional sensitivity. This directional sensitivity may be described by a cone of acceptance with specific horizontal and vertical dimensions. This acceptance cone will determine how the position, number, and distribution of artificial sources will affect an animal's orientation. Dim sources that are numerous and widely separated may have the same effect on orientation as a single bright source because hatchling sea turtles tend to move in the brightest direction as measured with a broad, flat acceptance cone.

(5) An animal may depend upon variously weighted multiple cues for correct orientation. Although highly directed artificial light fields can overwhelm these cues, it is important to understand how additional cues can help correct orientation that is affected by lighting. In hatchling sea turtles, the addition of shape cues can sometimes override their tendency to move in the brightest direction.

Conservation strategies for photopollution

An initial step in a conservation strategy is to identify areas where the potential for photopollution problems exist. Some of these areas have been identified: (1) where lighting is visible from sea turtle nesting beaches during the nesting and hatching season; (2) where lighting is located near the seaward route taken by fledging procellariiform birds; (3) where high-intensity lighting, especially up-lighting, is located along fall and spring migration routes of passerines; (4) at towers with aircraft warning lighting; (5) at lighthouses; and (6) at industrial oil flares. There are many other areas where nocturnal animals are affected by photopollution (e.g., insects at street lights, polychaetes in lighted harbors), although the consequences of these events are poorly understood. Research is sorely needed.

Mortality from photopollution can be both cryptic and variable in time. Consequently, the lack of discovery of dead animals at a lighted site does not exculpate a site of photopollution problems and it may be necessary to initiate light management at sites where photopollution problems are merely suspected.

After photopollution problems are identified, a light management plan can be enacted. Light management is more readily accepted as a conservation strategy than is simply prohibiting light within an area of concern. With proper light management, light sources are altered so that human needs for lighting are met and disruption of animal behavior is minimized. The following are some important considerations for light management.

Timing

Many animals are affected by photopollution only during critical periods. For sea turtles, the nesting and hatching period is critical. In the tropics this period varies, but at more temperate latitudes it usually occurs from late spring through early fall. For shearwaters and petrels autumn

fledging is a vulnerable time. For passerines most mortalities occur during spring and fall migrations. Restrictions on lighting during these periods are most important. Both birds and sea turtles are most vulnerable on cloudy and moonless nights (Verheijen 1981; Salmon & Witherington 1995).

Reducing perceived directivity and intensity

Other than turning light sources off, the principal way to reduce both intensity of a photopollution source (which may have many individual light sources) and its contribution to light field directivity is to reduce the power of constituent light sources. Lowering the wattage of luminaires will usually lower their contribution to a photopollution hazard but it will also reduce light that may be required for human activity. A way to reduce the photopollution hazard from a source while maintaining adequate levels of useful light is to restrict the distribution of light from the sources. Focusing a light source toward the ground can reduce the amount of errant light and decrease the directivity of the resulting light field as it is perceived by animals outside the immediate vicinity. Other useful techniques to control the escape of light include lowering pole-mounted luminaires, recessing lights into eaves, and shielding them. The use of light shields has reduced mortality at sea turtle nesting beaches and near shearwater and petrel nesting colonies. Although shields can be easily fashioned from any opaque material, luminaires specifically designed to eliminate stray light (e.g., cut-off luminaires) are a more efficient solution. Diffusing light from point sources by adding globes and other diffusers may decrease their attractiveness to insects but does not reduce their attractiveness to sea turtles.

Using light screens

In some situations, a 'non-point-source' glow affecting a specific area can be addressed by the use of light screens. For example, blocking distant city light from urban sea turtle nesting beaches has been shown to be helpful (Salmon *et al.* 1995). Although constructing opaque screens on the dune would suffice, preserving natural dune vegetation is a more permanent solution. Problems with photopollution are exacerbated at nesting beaches with a low dune profile and little dune vegetation.

Altering spectral properties

Often, the spectral sensitivity profiles of species that are affected by artificial lighting are different from the spectral requirements of humans. Birds are not sensitive to ultraviolet light and bird mortality at airport ceilometers has been essentially eliminated where ultraviolet sources have replaced white-light sources in ceilometer beams. Unfortunately, birds have a spectral range that is broader than ours (Norren 1979), leaving it difficult or impossible to select a colored light source that humans see well but that birds see poorly. Compared with humans, sea turtle spectral sensitivity is lower in the yellow-red end of the spectrum. Yellow, low-pressure-sodium-vapor luminaires, therefore, are good alternatives to broad-spectrum lighting on sea turtle nesting beaches (Witherington 1992*a*; Witherington & Bjorndal 1991*b*). Incandescent lamps that have been tinted to reduce blue emission (marketed as 'bug lights' because of their reduced attraction to insects) are also good alternatives to white sources. These colored sources, however, can affect sea turtles to some degree and should be shielded from beaches. Both low-pressure-sodium-vapor lighting and yellow bug lights kill substantially fewer nocturnal insects than other commercial sources. As a bonus, low-pressure-sodium-vapor sources are the most energy-efficient of all commercial sources, and they provide little interference with astronomical observation (because of the ease with which their monochromatic light can be filtered).

Reducing light duration

The motion-detector switch has been an important technological innovation for the management of security lighting. These switches activate a light source only when it is approached and can reduce the time that the light source affects animals. Work with sea turtles has shown that flashing lights are much less attractive than constant light sources, which suggests that hatchlings may integrate their measure of brightness over time (Mrosovsky 1978). In Australia, flashing lights have been deployed to mark paths to sea turtle nesting beaches. On many communications towers, constant or slow-pulse blinking lights for warning aircraft have been replaced by flashing strobes which has resulted in reductions in bird mortalities (Verheijen 1985). Similar reductions in bird kills have been observed at lighthouses where a flashing light has replaced a rotating beam.

Providing additional orientation cues

Ensuring that dunes at sea turtle nesting beaches remain vegetated will help provide additional shape cues to hatchlings and may help hatchlings correct orientation that is affected by artificial lighting. Verheijen (1985) suggests that using downward-directed flood lighting to brighten obstacles near towers may help reduce bird collisions by decreasing the directivity of the light field perceived by birds. A similar strategy of lighting the ocean at sea turtle nesting beaches would not be a solution to photopollution problems there. Light sources on the water could attract swimming hatchlings and cause hatchlings on adjacent stretches of beach to move parallel to the shore (Witherington 1991).

Public enlightenment

Photopollution problems on Florida sea turtle nesting beaches began to be recognized when workers in the field published details of sea-finding disruption and hatchling mortality they had observed. Awareness spread as biologists working at various nesting beach sites shared their concerns with the news media and members of the public. A biological interpretation of hatchling mortality events allowed the media to correctly interpret hatchling misdirection as the result of artificial lighting, rather than the result of more fanciful causes. Local residents and governmental officials in Florida became impressed when orientation and mortality problems were demonstrated in their areas. At an important Loggerhead and Green turtle nesting beach in Brevard County, Florida, public recognition of hatchling mortality became widespread following numerous news articles and editorials in the local media in the early 1980s. By 1985 Brevard County had promulgated the first local ordinance restricting lighting of the beach during the nesting season. Other coastal communities in Florida followed suit, and at present most of the Florida counties and municipalities near nesting beaches have ordinances designed to protect sea turtles from the effects of artificial lighting.

In some areas of heavily developed coastal Florida, substantial photopollution problems persist. In Dade and Broward counties (located in southeast Florida) most sea turtle nests are relocated to hatcheries that confine hatchlings as they emerge so that they can be gathered and released at dark-beach sites. Most sea turtle biologists believe that this strategy creates problems for hatchling survivorship. An important prob-

lem stemming from this technique is the illusion that the artificial lighting problem has been resolved.

In Florida and South Carolina, USA, involvement of local power companies has proven to be an important way to reach the public. Florida power companies have funded educational pamphlets and have begun the practice of including educational materials in the power bills sent to coastal consumers. In the USA, Costa Rica, Greece, and Australia, seaside resorts distribute information on how beach visitors can minimize the effects of lighting on sea turtles.

Bird kills at lighted structures are poorly known by the public considering the widespread nature of the phenomenon. Some specific cases, however, have enjoyed considerable attention such as the mortality of Hawaiian petrels and shearwaters (Reed *et al.* 1985). Deaths of these birds were substantially reduced after each of the entities responsible for the harmful lighting became convinced that their light management efforts would result in reduced bird mortality.

Elsewhere, serendipity more than design has been responsible for bird-friendly changes in light sources. The flashing strobes on modern communication and navigation towers are used primarily for their effectiveness in attracting human attention (thus deterring aircraft strikes and ship groundings). If experimental evidence confirms what anecdotal observations suggest, replacement of constant or blinking sources with strobes may be an important effort for migrating bird conservation. Many tall structures remain lighted with sources that can cause bird kills. Many of these are public facilities, so it may be most useful to concentrate efforts to resolve these conservation problems at a governmental level rather than at individual facilities.

Light management is likely to be most successful when initiated at the project-planning level. Light management is cheaper, more effective, and generally more palatable to developers when solutions are engineered into plans rather than retrofitted. Nonetheless, methods to reduce the effects from existing light sources abound and include options that generally are of minimal cost and inconvenience.

Continued research aimed at understanding behaviors affected by photopollution is essential for the development and testing of methods to mitigate the effects of artificial lighting. Solutions to lighting problems will need to be supported by research if they are to be embraced by development planners, governmental officials, and the public.

The role of conservation behaviorists

Although some conspicuous examples of behavioral modification and mortality from photopollution are known, many important effects are not likely to be discovered without considerable effort. Studies are needed that would elucidate the ecological effects of photopollution. Effects are sure to exist, whether large or small, almost anywhere that artificial light sources are positioned outdoors. Dark areas where artificial sources are scheduled to be introduced would provide unique opportunities for experimental discovery. This field provides an opportunity for behaviorists to make important contributions to conservation biology.

As natural areas are developed, the potential for biological photopollution is likely to increase. Of the many effects of human habitation on organisms, the effects from photopollution may be among the most readily managed. With the many techniques available for using light while minimizing its effects on nocturnal animals, the control of biological photopollution should be among the most prominent conservation success stories. The work of behavioral conservation biologists can help make this so.

Literature cited

Aldrich, J. W., R. R. Graber, D. A. Munro, G. J. Wallace, G. C. West, and V. H. Cahalane. 1966. Report of committee on bird preservation. *Auk* **83**: 465–467.

Ali, A., G. Ceretti, L. Barbato, G. Marchese, F. D'Andrea, and B. Stanley. 1994. Attraction of *Chironomus salinarius* (Diptera: Chironomidae) to artificial light on an island in the saltwater lagoon of Venice, Italy. *Journal of the American Mosquito Control Association* **10**: 35–41.

Baker, R. R. 1987. Integrated use of moon and magnetic compasses by the heart-and-dart moth, *Agrotis exclamationis*. *Animal Behaviour* **35**: 94–101.

Ben-Yami, M. 1976. *Fishing with light*. Fishing News Books, London.

Bjorge, R. R. 1987. Bird kill at an oil industry flare stack in northwest Alberta. *Canadian Field Naturalist* **101**: 346–350.

Clarke, M. R., P. L. Pascoe, and L. Maddock. 1986. Influence of 70 watt electric lights on the capture of fish by otter trawl off Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **66**: 711–720.

Dahiya, A. S., W. B. Tshernyshev, and V. M. Afronia. 1993. Diurnal rhythm of emergence from pupae in parasitic wasp *Trichogramma evanescens* Westw. (Insecta: Hymenoptera). *Journal of Interdisciplinary Cycle Research* **24**: 162–170.

Dick, M. H., and W. Donaldson. 1978. Fishing vessel endangered by crested auklet landings. *Condor* **80**: 235–236.

Foa, A. and G. Saviozzi. 1990. Effects of exogenous melatonin on sun-compass orientation of homing pigeons. *Journal of Biological Rhythms* **5**: 17–24.

Fong, P. P. 1993. Lunar control of epitokal swarming in the polychaete *Platynereis bicanaliculata* (Baird) from central California. *Bulletin of Marine Science* **52**: 911–924.

Granda, A. M., and P. J. O'Shea. 1972. Spectral sensitivity of the green turtle (*Chelonia mydas mydas*) determined by electrical responses to heterochromatic light. *Brain Behavior and Evolution* **5**: 143–154.

Howell, J. C., A. R. Laskey, and J. T. Tanner. 1954. Bird mortality at airport ceilometers. *Wilson Bulletin* **66**: 207–215.

James, P. 1956. Destruction of warblers on Padre Island, Texas, in May, 1951. *Wilson Bulletin* **68**: 224–227.

Kemper, C. A., D. G. Raveling, and D. W. Warner. 1966. A comparison of the species composition of two TV tower killed samples from the same night of migration. *Wilson Bulletin* **78**: 26–30.

Limpus, C. J. 1971. Sea turtle ocean finding behaviour. *Search* **2**: 385–387.

McFarlane, R. W. 1963. Disorientation of loggerhead hatchlings by artificial road lighting. *Copeia* **1963**: 153.

Mortimer, J. A. 1979. Ascension Island: British jeopardize 45 years of conservation. *Marine Turtle Newsletter* **10**: 7–8.

Mrosovsky, N. 1972. The water-finding ability of sea turtles. *Brain Behavior and Evolution* **5**: 202–225.

Mrosovsky, N. 1978. Effects of flashing lights on sea-finding behavior of green turtles. *Behavioral Biology* **22**: 85–91.

Mrosovsky, N., and S. F. Kingsmill. 1985. How turtles find the sea. *Zeitschrift für Tierpsychologie* **67**: 237–256.

Mrosovsky, N., and S. J. Shettleworth. 1968. Wavelength preferences and brightness cues in the water finding behaviour of sea turtles. *Behaviour* **32**: 211–257.

Mrosovsky, N., and S. J. Shettleworth. 1975. On the orientation circle of the leatherback turtle, *Dermochelys coriacea*. *Animal Behaviour* **23**: 568–591.

Norren, D. van. 1979. Two short wavelength sensitive systems in pigeon, chicken, and daw. *Vision Research* **15**: 1164–1166.

Pedgley, D. E., and S. Yathom. 1993. Windborne moth migration over the Middle East. *Ecological Entomology* **18**: 67–72.

Peters, A., and K. J. F. Verhoeven. 1994. Impact of artificial lighting on the seaward orientation of hatchling loggerhead turtles. *Journal of Herpetology* **28**: 112–114.

Philibosian, R. 1976. Disorientation of hawksbill turtle hatchlings, *Eretmochelys imbricata*, by stadium lights. *Copeia* **1976**: 824.

Reed, J. R., J. L. Sincock, and J. P. Hailman. 1985. Light attraction in endangered procellariiform birds: reduction by shielding upward radiation. *Auk* **102**: 377–383.

Rhijn, F. A. van. 1979. Optic orientation in hatchlings of the sea turtle, *Chelonia mydas*. I. Brightness: not the only optic cue in sea-finding orientation. *Marine Behavior and Physiology* **6**: 105–121.

Rhijn, F. A. van and J. C. van Gorkom. 1983. Optic orientation in hatchlings of the sea turtle, *Chelonia mydas*. III. Sea-finding behaviour: the role of photic and visual orientation in animals walking on the spot under laboratory conditions. *Marine Behavior and Physiology* **9**: 211–228.

Salmon, M. and B. E. Witherington. 1995. Artificial lighting and seafinding by loggerhead hatchlings: evidence for lunar modulation. *Copeia* **1995**: 931–938.

Salmon, M., M. G. Tolbert, D. P. Painter, M. Goff, and R. Reiners. 1995. Behavior of loggerhead sea turtles on an urban beach. II. Hatchling orientation. *Journal of Herpetology* **29**: 568–576.

Salmon, M., J. Wyneken, E. Fritz, and M. Lucas. 1992. Seafinding by hatchling sea turtles: Role of brightness, silhouette and beach slope as orientation cues. *Behaviour* **122**: 56–77.

Schacht, W., and T. Witt. 1986. Warum nachtaktive Insekten kuenstliche Lichtquellen anfliegen (Insecta). *Entomofauna* **7**: 121–128.

Schöne, H. 1984. *Spatial orientation*. Princeton University Press, Princeton, New Jersey.

Simons, T. R. 1984. A population model of the endangered Hawaiian dark-rumped petrel. *Journal of Wildlife Management* **48**: 1065–1076.

Stahlbaum, C. C., C. Rovee-Collier, J. W. Fagen, and G. Collier. 1986. Twilight activity and antipredator behavior of young fowl housed in artificial or natural light. *Physiology and Behavior* **36**: 751–758.

Syms, P. R., and L. J. Goodman. 1987. The effect of flickering U-V light output on the attractiveness of an insect electrocutor trap to the house-fly, *Musca domestica*. *Entomologia Experimentalis et Applicata* **43**: 81–86.

Takahashi, F., and A. Haruta. 1986. A portable automatic light trap and its application. *Kontyu* **54**: 373–380.

Verheijen, F. J. 1958. The mechanisms of the trapping effect of artificial light sources upon animals. *Archives Neerlandaises de Zoologie* **13**: 1–107.

Verheijen, F. J. 1981. Bird kills at tall lighted structures in the USA in the period 1935–1973 and kills at a Dutch lighthouse in the period 1924–1928 show similar lunar periodicity. *Ardea* **69**: 199–203.

Verheijen, F. J. 1985. Photopollution: artificial light optic spatial control systems fail to cope with. Incidents, causations, remedies. *Experimantal Biology* **44**: 1–18.

Verheijen, F. J., and J. T. Wildschut. 1973. The photic orientation of sea turtles during water finding behaviour. *Netherlands Journal of Sea Research* 7: 53–67.

Wada, T., H. Seino, Y. Ogawa, and T. Nakasuga. 1987. Evidence of autumn overseas migration in the rice planthoppers, *Nilaparvata lugens* and *Sogatella furcifera*: analysis of light trap catches and associated weather patterns. *Ecological Entomology* **12**: 321–330.

Witherington, B. E. 1991. Orientation of hatchling loggerhead turtles at sea off artificially lighted and dark beaches. *Journal of Experimental Marine Biology and Ecology* **149**: 1–11.

Witherington, B. E. 1992*a*. Behavioral responses of nesting sea turtles to artificial lighting. *Herpetologica* **48**: 31–39.

Witherington, B. E. 1992*b*. Sea-finding behavior and the use of photic orientation cues by hatchling sea turtles. Ph.D. dissertation, University of Florida, Gainesville. UMI Dissertation Information Service, Ann Arbor.

Witherington, B. E., and K. A. Bjorndal. 1991*a*. Influences of wavelength and intensity on hatchling sea turtle phototaxis: implications for sea-finding behavior. *Copeia* **1991**: 1060–1069.

Witherington, B. E., and K. A. Bjorndal. 1991*b*. Influences of artificial lighting on the seaward orientation of hatchling loggerhead turtles (*Caretta caretta*). *Biological Conservation* **55**: 139–149.

Witherington, B. E., K. A. Bjorndal, and C. M. McCabe. 1990. Temporal pattern of nocturnal emergence of loggerhead turtle hatchlings from natural nests. *Copeia* **1990**: 1165–1168.

Witherington, B.E. 1997. The problem of photopollution for sea turtles and other nocturnal animals. Chapter 13 in: J. R. Clemmons and R. Buchholz (eds.), Behavioral Approaches to Conservation in the Wild. Cambridge University Press, Cambridge. Pp. 303-328.