

## Sun Compass Orientation by Juvenile Green Sea Turtles (*Chelonia mydas*)

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**ABSTRACT.** – Juvenile green turtles occupy home ranges on shallow reefs that parallel the southeastern coast of Florida. When disturbed, the turtles often flee eastward toward deeper water. We captured turtles at night and recorded their orientation during the next 2 days while they swam tethered inside a large circular outdoor pool and were exposed to the sun. The turtles from 2 reef sites were significantly oriented eastward. After 7–10 days of exposure to a laboratory photocycle advanced by 7 hours, turtles tested in the same pool were significantly oriented westward, the predicted direction if they used the sun for orientation. Westward orientation was unaffected by placing either disc magnets or brass discs of identical mass above the turtles' heads. These results are consistent with the hypothesis that orientation under clear skies is preferentially based upon solar cues. However, control turtles exposed for 7–10 days to a photocycle advanced by 1 hour were also expected to swim generally eastward, but, for unknown reasons, failed to show significant orientation. Our results therefore support the hypothesis that the sun is used as a compass, but additional experiments will be required to provide definitive evidence.

**KEY WORDS.** – Reptilia; Testudines; Cheloniidae, *Chelonia mydas*, green turtle; sun compass; orientation; escape behavior

Many animals execute oriented movements using an external reference that serves as a compass. Common examples are compasses based upon the earth's magnetic field, the sun's azimuth, the polarized light pattern during the day, or the pattern of celestial (star) rotation at night (Rozhok 2008; Wiltschko and Wiltschko 2009). Among migrating birds, the best-studied group by far, alternative compasses are used during different portions of the journey or when weather conditions change (Able 1991). But, with the exception of the birds, little research has been conducted on other migratory animals to determine what kinds of compasses are used and how their use varies depending upon ecological circumstances.

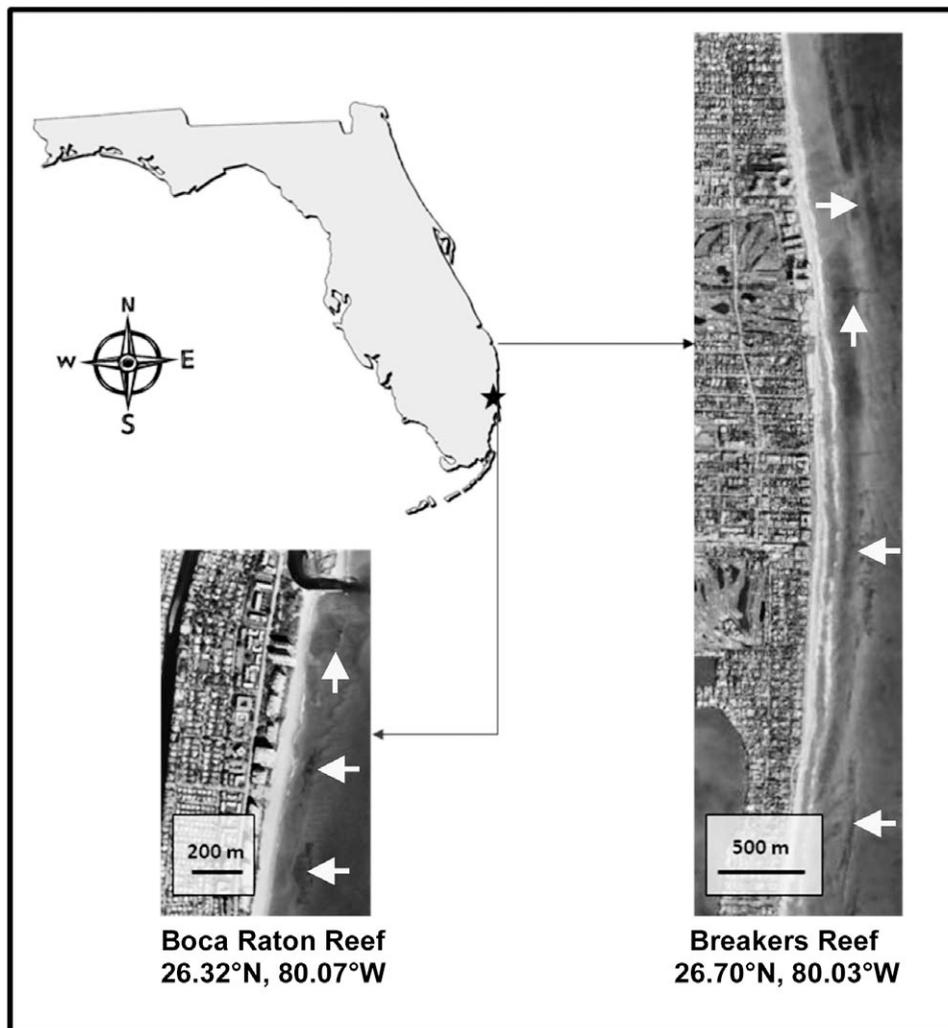
Sea turtles are excellent candidates for such a study because throughout their development these animals are known to use different compasses during orientation and migration. Loggerhead hatchlings (*Caretta caretta*), for example, use alternative visual cues (horizon elevation; differences in light intensity; Limpus 1971; Mrosovsky 1972; Salmon et al. 1992) to crawl directly from the nest to the ocean, but once they enter the sea, nonvisual compasses are employed. Offshore orientation is accomplished initially by swimming into surface waves (Salmon and Lohmann 1989; Wyneken et al. 1990) and is followed by orientation based upon a magnetic compass (Goff et al. 1998).

Juvenile loggerheads, hawksbills (*Eretmochelys imbricata*) and green sea turtles (*Chelonia mydas*) occupy temporary, and often spatially separated, "developmental habitats" for a sufficient time to establish home ranges. Their movements suggest that they "know" the location of essential resources (such as feeding or resting sites; van

Dam and Diez 1998, Seminoff et al. 2002, Makowski et al. 2006, Seminoff and Jones 2006) within those sites, although the mechanisms used to orient within those locations (possibly landmarks, possibly compasses, perhaps combinations of both) remain unknown.

Recent experiments also show that juvenile (Lohmann et al. 2004) and adult (Luschi et al. 2007) green turtles use magnetic cues both to navigate and to orient toward actual or perceived distant locations. However, alternative compasses are used when a magnetic compass cannot be used. For example, female green turtles bearing magnets and displaced from their nesting beach still return home (Luschi et al. 2007). Experiments with juvenile loggerhead sea turtles led to similar conclusions. When these turtles are captured at a distant site and then tethered inside outdoor tanks, they also swim toward the capture site before, as well as after, magnets are attached to their heads. They behave similarly when fitted only with frosted goggles (eliminating visual detail but not light stimulation). However, homeward orientation is abolished when the turtles bear both magnets and frosted goggles (Avens and Lohmann 2003). These results confirm that more than one compass is used and suggest that the alternative to the magnetic compass might be a visual compass.

In this study, we did experiments to determine whether the sun might serve as that visual compass. Solar compasses are commonly used to guide the daily as well as seasonal movements of many mobile animals (reviews in Dingle 1996; Rozhok 2008; Wiltschko and Wiltschko 2009), including some terrestrial and freshwater turtles (literature summarized in Graham et al. 1996). To date,



**Figure 1.** Shallow-water reefs where the turtles were captured. At both sites the reefs (dark patches or bands) are highlighted by white arrows. Star (upper diagram) shows the approximate location of the Florida Atlantic University Marine Laboratory.

only one study on sun compass orientation has been done using marine turtles. Fischer (1964) hypothesized that young green turtles used the sun for orientation and claimed that entrainment to a new light cycle predictably changed their directional preference. Such a change is expected when solar cues are used but Fischer presented no data to support his claim.

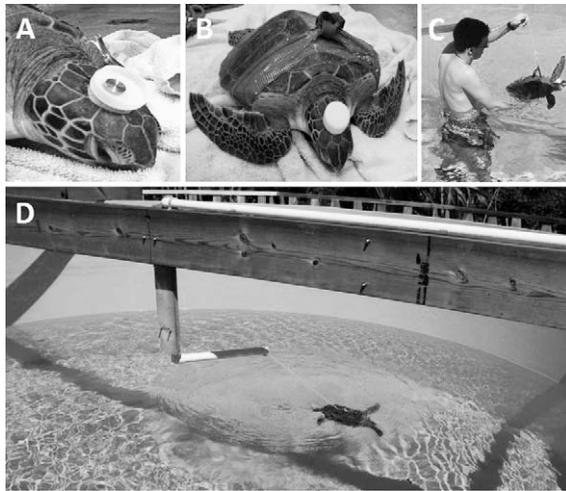
Our subjects were juvenile green turtles, which are common inhabitants of the shallow reefs that parallel the shore in southeastern Florida. These turtles frequently encounter swimming humans, but perhaps because of a historic turtle fishery, they are also wary and avoid close encounters by swimming away, often toward deep water. We captured juvenile turtles over the reef at night and tested their orientation during the daylight hours in a large outdoor tank with no view of the ocean, but with a clear view of the sun. The turtles oriented offshore (east to northeast), but after a week's exposure to a light cycle advanced by 7 hours, orientation was predictably shifted to the west or northwest. Magnets placed on the turtles did not alter this orientation shift. These results suggest that

offshore orientation might be mediated by a solar compass.

## METHODS

*Capture, Maintenance, and Release of Turtles.* — Between May and October 2009, juvenile green turtles were hand-captured at night by divers using SCUBA over shallow (2–6-m-deep) reefs that parallel the shoreline in areas of Palm Beach County, Florida (Fig. 1). One reef was located ~ 37 km to the north (the Breakers reef) and the other, ~ 5 km to the south (Boca Raton reef) of the Florida Atlantic University (FAU) Marine Laboratory in Boca Raton, Florida, where all of the experiments were done.

The day after capture, each turtle was weighed (nearest 0.1 kg) using a net and spring scale (Model 2012, Manley Industries, Lakewood, NJ) and measured (straight-line carapace length [SCL], to nearest 0.1 cm) using calipers. External parasites and epibiota (leeches and barnacles), if present, were removed. Minor abrasions



**Figure 2.** Procedures for measuring turtle orientation. A, A round plastic box was glued to the turtle's parietal scales. During experiments, the box contained either brass discs (shown here) or magnets of identical mass and shape. B, Turtle in its duct-tape harness, with the plastic box lid closed. Loop of spandex cloth is wrapped within the harness and used for tether attachment. C, Turtle is attached to a tether connected to the rotating arm that registers its swimming direction. D, Turtle swimming during its trial.

were treated with antibiotic ointment. All of the turtles used in tests were in excellent condition. Six turtles were usually captured on the same evening and then isolated individually in round, plastic laboratory tanks (1.78 m diameter  $\times$  1.22 m deep; capacity of 1891 L) continuously supplied with filtered seawater. The tanks were positioned in 2 adjacent rows of 3 tanks each, with each tank illuminated by 2 full-spectrum fluorescent tubes (ReptiSun<sup>®</sup> 5.0 and 10.0, ZooMed). The rows were isolated from one another by black plastic sheeting so that each row of tanks could be simultaneously exposed to a different light cycle controlled by timers. However, for the first 2 days after capture, the tank light cycle matched the ambient light cycle (lights on 30 minutes before sunrise and off 30 minutes after sunset).

While the lights were on, the turtles were fed once daily using a temporally irregular schedule. The diet consisted of romaine, red leaf, and green leaf lettuce supplemented with raw squid, fish, and shrimp (2%–5% of body weight daily; Witham and Furch 1977, Higgins 2003). A hollow concrete block was placed in each tank to simulate a ledge similar to the kind used by turtles as a nighttime resting site. The turtles were otherwise left undisturbed except for daily tank cleaning to remove feces and excess food. Turtles ate irregularly during their first week in captivity but later fed aggressively. All turtles gained weight by the time their period in captivity ended (within 3 weeks after capture).

Turtles were released during the day within a few hundred meters of their capture site. Just prior to their release, a flipper tag (Model 1005-681, Inconel) was placed on the trailing edge of each front flipper and a

passive identification tag (Model TX1406L, Destron-Fearing) was inserted into the musculature of the right front shoulder. Released turtles were frequently seen again during our nighttime searches for new turtles.

**Orientation Tank.** — Tests were done in an outdoor custom-built circular fiberglass tank located at the FAU laboratory, about 200 m from the beach. The tank measured 6.10 m in diameter and 2.44 m deep (capacity = 71,308 L). It was painted light blue and filled to a depth of 1.4 m with filtered seawater. At water level, the turtles had an  $\sim 70^\circ$  view around the zenith that included the tops of 2 canopy awnings over adjacent tanks to the southwest, the crowns of 2 palm trees to the west, and an overhead supporting beam (oriented on a southwest to northeast axis) used to suspend a rotating lever arm just above the water surface in the center of the tank (Fig. 2).

The tank wall consisted of 4 vertical sections sealed together and reinforced from top to bottom with stainless steel bolts. Those bolts weakly distorted the magnetic field near the seams but their magnetic influence could not be detected (with a Schonstedt Model DM 2220 fluxgate magnetometer) more than 1.0 m away from the wall. Within that central area, the horizontal and vertical components of the earth's field were virtually identical to those measured at the beach. The turtles were confined to that central area by a short lever arm, plus a 1-m-long nylon rope tether that limited the distance that the turtles could swim from the center of the tank to  $\sim 2.0$  m. That system, however, placed no limit on the turtle's swimming direction.

**Testing Protocol.** — Each turtle was prepared for tests using the following procedures. First, each turtle was removed from its indoor tank and patted dry with a soft towel. A circular patch of soft Velcro<sup>®</sup>,  $\sim 3.0$  cm in diameter, was attached by its adhesive surface to the turtle's parietal scales; a small hollow plastic box with Velcro hooks glued to the bottom was then secured to the patch (Fig. 2A). This "head box" (3.3 cm diameter  $\times$  2.0 cm high; mass,  $\sim 8.0$  g) was used in experiments (see below) to contain either 2 small disc-shaped neodymium magnets stacked together (Model D82E, K & J Magnetics) or a pair of brass discs of identical shape and mass (Fig. 2B).

Each turtle was also fitted with a temporary harness made with several wraps of heavy-duty duct tape around the body, just behind the front flippers (Fig. 2B). A loop of spandex cloth was inserted within the tape harness at the dorsal midline and served as a point of attachment for the nylon rope tether. The turtle was then carried a short distance outdoors, placed inside the tank, and connected to the lever arm by the tether (Fig. 2C). This arrangement allowed the turtle to swim in the central area of the tank and pull the rotating arm behind it (Fig. 2D). A digital encoder (S1-360-250-I-B-S, U.S. Digital) linked to the arm continuously recorded the turtle's swimming direction.

Once the turtle was attached to its tether, it was released in one of 4 cardinal directions and left alone in the tank for a 1-hour trial. Its orientation was recorded every 30 seconds during the last 15 minutes of the trial. The data were stored on a computer located in an adjacent shed.

At the conclusion of the trial, the turtle was removed from the tank, relieved of its harness and “head box” (by peeling the cloth Velcro from its parietal scales), and returned to its laboratory holding tank.

Because thunderstorms often occurred during the afternoon all swimming trials were done between 0845 hours and 1400 hours, when the sky was generally clear and the sun was only briefly obscured by occasional clouds.

*Initial Trials and Later Experimental Tests.* — To determine if the turtles oriented in a consistent direction, an initial orientation trial was done within 48 hours after capture. During this trial the head box (with its lid closed) was attached to the turtles’ parietal scales, but left empty.

Experimental tests were done 7–10 days later after 3 turtles in one row of tanks were entrained to a light cycle advanced by 1 hour (controls) and 3 turtles in the adjacent row were entrained to a light cycle advanced by 7 hours (experiments). Each turtle was then given 2 tests (1 each day for 2 days). During one test, the head box contained magnets; during the other it contained brass discs. Tests were balanced so that half of the turtles were first tested with the magnets and half were first tested with the brass discs. When another group of 6 turtles was captured, the control and experimental turtles were housed in different rows of tanks.

The fluxgate magnetometer was used to measure the distortion of earth’s magnetic field produced by the magnets. Measurements were made as a function of horizontal distance (in 5-cm steps) until the values no longer differed from background.

The experimental tests were designed to determine what compass cues the turtles used during their initial trial. If, for example, the turtles were using the sun for orientation, then entrainment to an advanced photocycle should cause them to shift their orientation in a counterclockwise direction relative to their orientation during the initial trial. The amount of that angular change was estimated by the change in the sun’s azimuth over a 7-hour period when the experiments were done (the average of the hourly change in the daily azimuth between May and October 2009). Azimuth plots were obtained from the National Oceanic and Atmospheric Administration online solar calculator (Earth Systems Research Laboratory, Global Monitoring Division, [www.esrl.noaa.gov/gmd/grad/socal/](http://www.esrl.noaa.gov/gmd/grad/socal/)).

However, if the turtles were using magnetic rather than solar cues for orientation, then clock shifting was predicted to have no effect on orientation because use of a magnetic compass does not require time-compensation. Thus, the orientation *direction* chosen by the turtles after

entrainment to an advanced photocycle should indicate whether a solar or a magnetic compass was being used.

Attaching magnets and brass discs to the turtles was done to determine if more than one compass could be used and if so, which was “preferred” (e.g., the “hierarchy” of compasses; Able 1991). For example when tested with brass discs in the head box, the turtles had the option of choosing either a magnetic or visual compass for orientation. However, when tested with magnets the turtles should have been unable to use directional information from the earth’s magnetic field. If they remained oriented, then they should do so using an alternative (and perhaps visual) compass (as in Avens and Lohmann 2003).

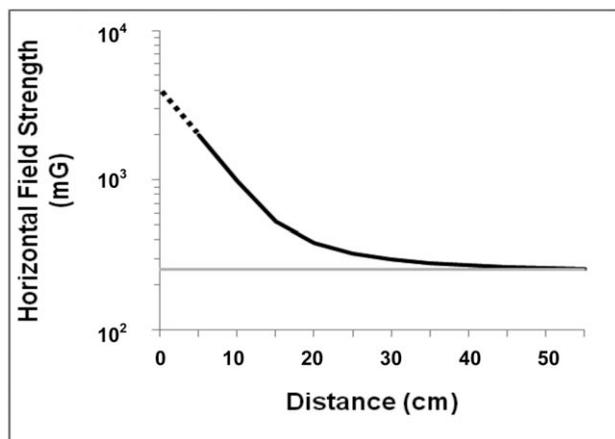
Turtles exposed to a 1 hour advance in the photocycle were included as controls to determine whether orientation was affected by laboratory confinement and/or exposure to an altered photocycle. Assuming there were no such adverse effects, we anticipated that the turtles in this group, whether tested with either brass or magnetic discs, would orient in directions similar to those chosen by turtles during their initial trial because the sun’s azimuthal change over a 1-hour period was, on average, relatively small. We expected that any such change would probably be obscured by variation among the turtles in their preferred orientation.

*Data Collection and Statistics.* — A software program (Arena Tracker) specifically developed for orientation studies (by W.P. Irwin, University of North Carolina, Chapel Hill, NC) was used to determine a mean angle of orientation for each turtle. Mean angles during the initial trials were initially pooled by the capture site (Breakers reef or Boca Raton reef) to determine a second-order mean angle and *r*-vector (measure of dispersion) for each distribution. Rayleigh tests were used to determine whether those distributions were significantly clustered. If they were, Watson tests were used to determine if the distributions from the 2 reef sites differed statistically (Zar 1999).

Rayleigh tests were also used to determine whether the control (1-hour-advanced light cycle) and experimental (7-hour-advanced cycle) turtles showed significant orientation. The magnet and brass groups were analyzed separately for both the control and experimental turtles. When significant orientation occurred, Watson tests were used to determine whether the 2 distributions under each entrainment regime differed statistically (Zar 1999).

The mean azimuthal change over a 1-hour and 7-hour period was used to predict the change in orientation that clock-shifted turtles should show if using the sun as a reference. A one-sample test for the mean angle (Zar 1999) was used to determine whether the predicted angular shift fell within the 95% confidence limits of the observed angular shift. If it did, then the observed and predicted angular changes were considered statistically identical.

*T*-tests (Zar 1999) were used to determine whether the SCL and mass measurements for the turtles captured at each reef site were statistically uniform.



**Figure 3.** Attenuation plot of horizontal magnetic field intensity generated by the disk magnets used in these experiments, plotted against distance. Dashed line in plot shows presumed values above the range of the magnetometer's sensitivity. Background intensity (gray line): 253 mG. Note that the magnets distort the earth's horizontal field over a distance exceeding 40 cm.

In all statistical tests, probabilities  $\leq 0.05$  were considered significant.

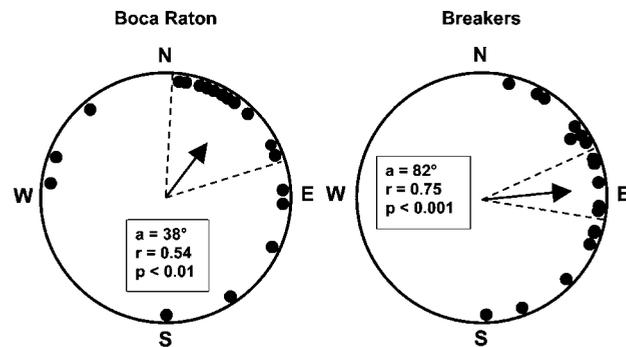
## RESULTS

**Turtles.** — Only juvenile green turtles ( $\leq 60.0$  cm) were seen on the reefs. At the Breakers site, turtles were encountered under or near the eastern reef ledges, or on the rubble from a collapsed pier extending to the east in front of the Breakers Hotel. At the Boca Raton site turtles were found resting on the bottom between artificial reef modules or under natural reef ledges. At both capture sites a few turtles were actively swimming over the reef at night.

All turtles were approached using bright underwater flashlights. Inactive turtles resting on the bottom were simply grasped and brought to the surface for transfer to a waiting boat. Active turtles were both curious and wary; they were most easily captured when one diver attracted their attention while another approached from the rear. Turtles that escaped from a diver's grasp repeatedly circled both divers from a safe distance; once alerted they could not be captured until later, after a return to the area.

In total, 21 juvenile green turtles were captured at the Boca Raton reef and 18 at the Breakers reef. The Boca Raton turtles were (mean  $\pm$  SD)  $38.1 \pm 10.16$  cm SD in SCL (range 25.9–59.2 cm) and  $8.73 \pm 7.67$  kg SD in mass. The Breakers turtles were slightly smaller:  $34.1 \pm 7.25$  cm SD in SCL (range 27.4–52.1 cm) and  $5.63 \pm 4.70$  kg SD in mass. Both size and mass were normally distributed. Turtles from the 2 sites did not differ statistically in either character (SCL,  $t = 1.37$ ,  $p = 0.18$ ; mass,  $t = 1.50$ ,  $p = 0.14$ ;  $df = 37$ ).

**Magnetic Measurements.** — The disc magnets placed on each turtle's head distorted the earth's magnetic field in the horizontal plane over a distance exceeding 40 cm, longer than the SCL of many of the turtles (Fig. 3).



**Figure 4.** Initial orientation shown by the Boca Raton ( $n = 19$ ) and Breakers reef ( $n = 17$ ) turtles tested within 48 hours of capture. Filled dots represent the mean angle of orientation by each turtle. The group mean angle ( $a$ ) is shown by the arrow whose length is proportional to the  $r$ -vector (dispersion). Dashed lines represent the 95% confidence interval for the mean angle. Both groups of turtles are significantly oriented. The 2 distributions are statistically identical (see text).

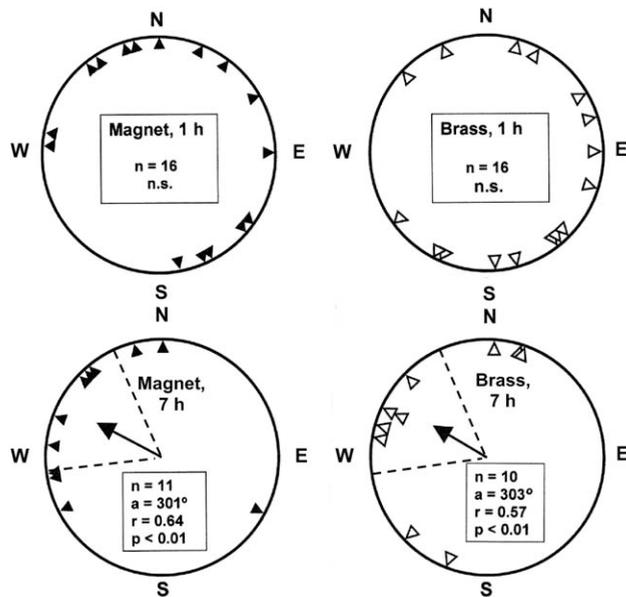
**Initial Orientation Trials.** — When released in the orientation tank, tethered turtles initially swam with vigor and made frequent dives of short duration. After about 10–15 minutes, the turtles stopped circling, swam more slowly, dove for longer periods, and oriented in a direction that was usually maintained for the rest of the trial. During the initial trials, the Boca Raton turtles ( $n = 19$ ; data lost for 2 turtles) on average headed northeast (95% CI:  $38^\circ \pm 31^\circ$  SD) whereas the Breakers turtles ( $n = 17$ ; data lost for 1 turtle) headed east-northeast ( $82^\circ \pm 21^\circ$  SD; Fig. 4). Both groups of turtles were significantly oriented. The two distributions did not differ statistically (Watson  $U^2 = 0.165$ , not significant) and so were pooled to yield a combined initial trial mean angle of  $63^\circ \pm 20^\circ$  SD.

**Orientation After Entrainment.** — Turtles entrained to a 1-hour advance in the light cycle and tested with magnets or brass discs failed to show significant orientation (Fig. 5, top diagrams). Turtles entrained to a 7-hour advance in the light cycle were significantly oriented (Fig. 5, lower diagrams), whether bearing magnets ( $301^\circ \pm 34^\circ$  SD) or brass discs ( $303^\circ \pm 42^\circ$  SD). The two distributions did not differ statistically and were pooled to yield a group mean angle of  $302^\circ \pm 26^\circ$  SD.

If the turtles exposed to a 7-hour advance in the light cycle were using the sun's azimuth as a reference, they should have, on average, shifted their orientation counterclockwise by  $\sim 145^\circ$  (Fig. 6). The predicted group mean angle was therefore  $145^\circ$  to the left of  $63^\circ$ , or  $278^\circ$ . The observed mean angle ( $302^\circ$ ) fell within the 95% confidence limits of  $278^\circ$  ( $\pm 26^\circ$  SD, or  $252^\circ - 304^\circ$ ).

## DISCUSSION

**Initial Orientation Trials.** — Green turtles used in the initial trials were well oriented (Fig. 4) but not in the directions that we anticipated. We hypothesized that the turtles captured at the Breakers reef might orient toward

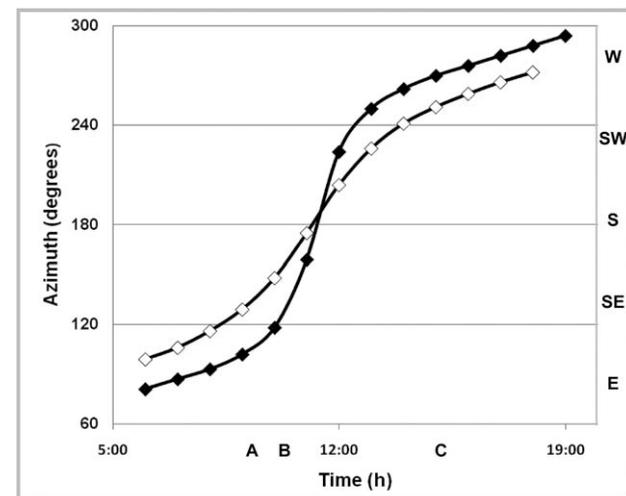


**Figure 5.** Results for the turtles entrained to different photoperiods for 7–10 days. Above, after a 1-hour advance; below, after a 7-hour advance. Tests after exposure to both light regimes were done twice (usually on consecutive days), once when magnets were inside the “head box” (left diagrams) and once when the box contained brass discs (right diagrams). The turtles showed no significant orientation after the 1-hour advance but were significantly oriented after the 7-hour advance. Dashed lines represent the 95% confidence interval for the mean angle.

home, as did the juvenile green turtles captured at a similar distance from the test site in a previous study (Avens and Lohmann 2004). We were uncertain about how the Boca Raton reef turtles would respond since they were captured so close (~ 5 km) to the location of the orientation trials. We found that both the Breakers reef and Boca Raton reef turtles were oriented in a statistically identical (generally eastward) direction, which in neither instance was toward their capture site. In fact, their behavior most closely resembled the y-axis orientation shown by amphipods (Scapini 2006; Forward et al. 2009) and terrestrial turtles (DeRosa and Douglas 1982) that direct animals on perpendicular courses away from suboptimal habitats, and toward more favorable habitats.

We hypothesize that the green turtles were showing an *escape response* toward offshore waters, behavior that could be advantageous for 2 reasons. First, there are additional reefs in deeper water that might provide cover in the form of hiding places. Second, in deeper water green turtles might better use their superior swimming speed and maneuverability (Heithaus et al. 2002, 2005) to either avoid or distance themselves from potential threats (historically, humans; currently, sharks).

Because virtually nothing is known about how turtles in our local population actually respond to their predators, the efficacy of such an escape strategy remains unknown. However, there is no question that functionally this response differs from the responses described in previous studies that demonstrate the turtles’ ability to determine



**Figure 6.** Hour-by-hour changes in the sun’s azimuth (left, in degrees measured from North) and in its geographic position (right) for May (filled diamonds) when experiments began, through October (open diamonds) when experiments ended. The distance between points A and B on the time scale (0900 to 1000 hours) indicates the azimuth angle change expected on the y axis (left) after entrainment to a 1-hour advance in the morning ( $\Delta_{\text{May}} = 16^\circ$ ;  $\Delta_{\text{Oct}} = 19^\circ$ ). The distance between points A and C (0900 to 1600 hours) indicates the azimuth angle change expected after a 7-hour advance in the light cycle ( $\Delta_{\text{May}} = 168^\circ$ ,  $\Delta_{\text{Oct}} = 122^\circ$ ; average =  $145^\circ$ ). Note that the sun’s azimuth over 7 hours changes from the southeastern to the southwestern portion of the sky.

their location relative to the capture site, and then to orient toward home (Avens and Lohmann 2004; Lohmann et al. 2004).

Why, then, did our turtles behaved so differently? The answer may be a function of the ecological setting. Our turtles occupy long, narrow home ranges for at least several months at a time, and perhaps longer (Makowski et al. 2006). These sites are located in clear, shallow water where the turtles feed on patches of algae located on brightly illuminated flat reefs that parallel the shoreline (Fig. 1). When threatened by a predator in such a habitat, escape options are probably limited. Moving into yet shallower water toward the surf zone provides no cover and probably compromises maneuverability. Swimming parallel to the shore (to the north or south) risks continued exposure over a flat reef optimal for algae growth, but without places to hide and therefore also devoid of cover (Fig. 1). Thus, the best option may be to swim offshore.

In contrast, the turtles studied by Lohmann et al. (2004) and by Avens and Lohmann (2004) were found in extensive and highly productive shallow bays where visibility was limited, and where resources such as food patches were probably spaced out rather than spatially concentrated. In such an environment, there may be a premium on an ability to “know” the area and to home to specific locations within the bay, but no advantage to an escape response in any particular direction. In that kind of ecological setting, an ability to return to the original encounter site might be especially favored.

Our results do not mean that green turtles from our population are incapable of homing. In an unpublished study, McDermott and Salmon (unpubl. data, 2004) tracked the movements of 3 juvenile green turtles captured at the Breakers reef after their release in deep water, 1.0–3.0 km away. Over several hours, all 3 returned to shallow water and from there, swam toward their capture site.

*Experimental Trials.* — The use of the sun for orientation is complicated by its change in both direction (azimuth) and elevation (altitude) throughout the day. Most organisms ignore changes in the sun's altitude, responding instead to the sun's azimuth (Hasler et al. 1958; Dingle 1996; Rozhok 2008; Wiltschko and Wiltschko 2009). The underlying mechanism is a biological "clock" that dictates a temporal schedule of compensation for the azimuth change (Wiltschko et al. 2000; Wiltschko and Wiltschko 2009). Following that schedule permits the animal to consistently orient in the same direction. At Boca Raton, for example, the azimuth changes slowly in the early morning and late afternoon, and rapidly during the midday. Patterns of daily variation also change seasonally. At the northern middle latitudes, hourly variation during the midday is largest during the summer solstice and declines toward the equinoxes as the sun's declination moves southward (Fig. 6). Since our trials were done as these changes progressed (May through October), we used the average seasonal rate of change to estimate by how much orientation would be affected by a 7-hour advance in the light cycle. That estimate was a counterclockwise shift of  $\sim 145^\circ$  (an expected mean angle of  $278^\circ$ ). The mean angle shown by the entrained turtles ( $302^\circ$ ) fell within the 95% confidence interval of that estimate.

Two methods have been used to demonstrate that a solar (or lunar) compass is used for orientation. One is to deflect the apparent location of the celestial body using mirrors (Kramer [1952] with birds; Enright [1961] with amphipods; Dacke et al. [2004] with beetles) and induce an immediate shift in orientation by the animal. Another method is to alter the animal's perception of time by entraining it to a new light cycle (the clock-shifting experiment) and then to also demonstrate a predictable change in orientation based upon the animal's azimuth compensation schedule at its perceived time (Schmidt-Koenig 1960, 1961; Wiltschko et al. 2000). In this study, we entrained the turtles to a light cycle advanced by 7 hours relative to local time, then exposed the turtles to the sun during the morning and early afternoon. However, to the entrained turtles, the "day" had started 7 hours earlier, and so they perceived their solar reference as an afternoon sun in the southwestern portion of the sky (Fig. 6). To escape to the east-northeast during the afternoon, turtles should orient *almost directly away* from the afternoon sun. Our turtles behaved as predicted because most of them oriented to the northwest, or almost directly away from the morning sun (Fig. 6).

Control turtles were exposed to a photocycle advanced by 1 hour. For reasons that we cannot explain, these turtles failed to show significant orientation (Fig. 5). Since the control turtles were tested at the same time and during the same days as the experimental subjects (trials of the control and experimental turtles alternated during each daily session), the failure of the controls to orient cannot be attributed to any differences associated with the time or place where testing occurred.

At the same time, the failure of the controls to orient was informative because it showed that 1) potential cues that might have been used to maintain vectors (palm trees and canopy awnings; the beam supporting the lever arm) were insufficient to account for the initial east-northeast performance of the turtles, and that 2) orientation performance was sensitive to even slight changes in the timing of the light-dark cycle. That sensitivity is characteristic of solar or lunar orientation (Schmidt-Koenig 1960, 1961; Enright 1961). These data are therefore *consistent* with the hypothesis that the turtles are using the sun as a reference, but clearly additional experiments (with control animals that orient as anticipated and with turtles tested under overcast skies) are required to demonstrate unequivocally that there is a *cause and effect* relationship between the sun's location and the turtles' orientation.

*Cues Mediating the Escape Response.* — We anticipated on the basis of previous work with juvenile loggerheads (Avens and Lohmann 2003) that when green turtles had magnets placed on their head they would rely on an alternative, and probably visual, compass (Avens and Lohmann 2003). That expectation was confirmed as after entrainment to a 7-hour light advance the turtles in the magnet group oriented as predicted if the sun was used as a guidepost (Fig. 5). However, turtles in the brass group also oriented to the northwest and their behavior, contrary to expectations, suggests that the escape response is *preferentially* mediated by nonmagnetic cues because even when magnetic cues were available, they were apparently not used. Perhaps magnetic cues are used when the sun is obscured by clouds or during escape responses performed at night. Further research will be required to provide the answers. But if the turtles are to respond immediately to threats encountered during the daylight hours, the sun is certainly an advantageous cue. It is almost always visible to an animal living in clear, shallow coastal waters off the east coast of Florida. In addition, its east-west arc across the sky makes it an especially useful reference for an animal whose movements are largely confined to reefs oriented north to south (Makowski et al. 2006).

Other marine animals are known to use the sun for orientation when they are threatened, or somehow find themselves in suboptimal habitats. Adult parrot fish (*Scarus guacamaia* and *Scarus coelestinus*) in Bermuda feed on algae growing on the surface of rocks in shallow-water bays. When alarmed they flee rapidly offshore

toward deep water reefs. Their orientation is mediated by the sun (Winn et al. 1964). The sun is also used by terrestrial amphipods living on beaches in southern Europe (*Talitrus*; Scapini 2006) and North Carolina (*Talorchestia*; Forward et al. 2009). These crustaceans orient toward land when waves carry them into predator-rich shallow waters, or (in *Talitrus*) toward moist sand when they are swept into excessively dry, hot sand farther away from the swash zone.

The role of solar orientation in the daily and periodic migratory movements of marine turtles remains unexplored. One possibility is that the sun is used in much the same way as in migratory birds. Diurnally migrating birds use geomagnetic rather than solar cues for orientation, probably because they move rapidly and with rapid changes in latitude, the sun's azimuth compensation schedule also shows a rapid change. However, having arrived at their destination (a breeding or an overwintering site), birds learn the local azimuth schedule. Birds may even remember 2 such learned schedules, one appropriate for their breeding and another for their overwintering site (Wiltschko and Wiltschko 2009). This functional arrangement might also apply to marine turtles that seasonally migrate between home ranges located at higher and lower latitudes (Avens and Lohmann 2004); studies to investigate this possibility remain obvious topics for future research.

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#### LITERATURE CITED

- ABLE, K.P. 1991. Common themes and variations in animal orientation systems. *American Zoologist* 31:157–167.
- AVENS, L. AND LOHMANN, K.J. 2003. Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta*. *Journal of Experimental Biology* 206:4317–4325.
- AVENS, L. AND LOHMANN, K.J. 2004. Navigation and seasonal migratory orientation of juvenile sea turtles. *Journal of Experimental Biology* 207:1771–1778.
- DACKE, M., BYRNE, M.J., SCHOLTZ, C.H., AND WARRANT, E.J. 2004. Lunar orientation in a beetle. *Proceedings of the Royal Society of London B* 271:361–365.
- DEROSA, C.T. AND DOUGLAS, H.T. (1982) A comparison of compass orientation mechanisms in three turtles (*Trionyx spinifer*, *Chrysemys picta* and *Terrapene carolina*). *Copeia* 2: 394–399.
- DINGLE, H. 1996. *Migration: The biology of life on the move*. Oxford: Oxford University Press, Inc, 474 pp.
- ENRIGHT, J.T. 1961. Lunar orientation of *Orchestoidea corniculata* Stout (Amphipoda). *Biological Bulletin Woods Hole* 120:148–156.
- FISCHER, K. 1964. Spontanes richtungsfinden nach dem sonnenstand bei *Chelonia mydas* L. (suppenschildkrote). *Naturwissenschaften* 51:203.
- FORWARD, R.B., BOURLA, M.H., LESSIOS, N.N., AND COHEN, J.H. 2009. Orientation to shorelines by the supratidal amphipod *Talorchestia longicornis*: wavelength specific behavior during sun compass orientation. *Journal of Experimental Marine Biology and Ecology* 376:102–109.
- GOFF, M., SALMON, M., AND LOHMANN, K.J. 1998. Hatchling sea turtles use surface waves to establish a magnetic compass direction. *Animal Behaviour* 55:69–77.
- GRAHAM, T., GEORGES, A., AND McELHINNEHY, N. 1996. Terrestrial orientation by the eastern long-necked turtle, *Chelodina longicollis*, from Australia. *Journal of Herpetology* 30:467–477.
- HASLER, A.D., HERRALL, R.M., WISBY, W.J., AND BRAEMER, W. 1958. Sun-orientation and homing in fishes. *Limnology and Oceanography* 3:353–361.
- HEITHAUS, M.R., FRID, A., AND DILL, L.M. 2002. Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. *Marine Biology* 140:229–236.
- HEITHAUS, M.R., FRID, A., WIRSING, A.J., BEJDER, L., AND DILL, L.M. 2005. The biology of sea turtles under risk from tiger sharks at a foraging ground. *Marine Ecology Progress Series* 288:285–294.
- HIGGINS, B.M. 2003. Sea turtle husbandry. In: Lutz, P.L., Musick, J.A., and Wyneken, J.W. (Eds.). *The Biology of Sea Turtles*. Volume II. Boca Raton, FL: CRC, pp. 411–440.
- KRAMER, G. 1952. Experiments on bird orientation. *Ibis* 94:265–285.
- LIMPUS, C.J. 1971. Sea turtle ocean finding behaviour. *Search* 2: 385–387.
- LOHMANN, K.J., LOHMANN, C.M.F., EHRHART, L.M., BAGLEY D.A., AND SWING, T. 2004. Geomagnetic map used in sea-turtle navigation. *Nature* 248:909–910.
- LUSCHI, P., BENHAMOU, S., GIRARD, C., CICCIONE, S., ROOS, D., SUDR, J., AND BENVENUTI, S. 2007. Marine turtles use geomagnetic cues during open-sea homing. *Current Biology* 17:126–133.
- MAKOWSKI, C., SEMINOFF, J.A., AND SALMON, M. 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, FL, USA. *Marine Biology* 148:1167–1179.
- MROSOVSKY, N. 1972. The water-finding ability of sea turtles. *Brain, Behaviour and Evolution* 5:202–225.

- ROZHOK, A. 2008. Orientation and navigation in vertebrates. Berlin: Springer, 164 pp.
- SALMON, M. AND LOHMANN, K.J. 1989. Orientation cues used by hatchling loggerhead sea turtles (*Caretta caretta* L.) during their offshore migration. *Ethology* 83:215–228.
- SALMON, M., WYNEKEN, J., FRITZ, E., AND LUCAS, M. 1992. Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. *Behaviour* 122:56–77.
- SCAPINI, F. 2006. Keynote papers on sandhopper orientation and navigation. *Marine and Freshwater Behaviour and Physiology* 39:73–85.
- SCHMIDT-KOENIG, K. 1960. The sun azimuth compass: one factor in the orientation of homing pigeons. *Science* 131:826–828.
- SCHMIDT-KOENIG, K. 1961. Sun navigation in birds? *Nature* 190:1025–1026.
- SEMINOFF, J.A. AND JONES, T.T. 2006. Diel movements and activity ranges of green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. *Herpetological Conservation Biology* 1:81–86.
- SEMINOFF, J.A., RESENDIZ, A., AND NICHOLS, W.J. 2002. Home range of the green turtle (*Chelonia mydas*) at a coastal foraging ground in the Gulf of Mexico. *Marine Ecology Progress Series* 242:253–265.
- VAN DAM, R.P. AND DIEZ, C.E. 1998. Home range of immature hawksbill turtles (*Eretmochelys imbricata* [Linnaeus]) at two Caribbean Islands. *Journal of Experimental Marine Biology and Ecology* 220:15–24.
- WILTSCHKO, R., WALKER, M., AND WILTSCHKO, W. 2000. Sun-compass orientation in homing pigeons: compensation for different rates of change in azimuth? *Journal of Experimental Biology* 203:889–894.
- WILTSCHKO, R. AND WILTSCHKO, W. 2009. Avian navigation. *Auk* 126:717–743.
- WINN, H.E., SALMON, M., AND ROBERTS, N. 1964. Sun-compass orientation by parrotfishes. *Zeitschrift für Tierpsychologie* 21:798–812.
- WITHAM, R. AND FUTCH, C.R. 1977. Growth and survival of pen-reared sea turtles. *Herpetologica* 33:404–409.
- WYNEKEN, J., SALMON, M., AND LOHMANN, K.J. 1990. Orientation by hatchling loggerhead sea turtles *Caretta caretta* L. in a wave tank. *Journal of Experimental Marine Biology and Ecology* 139:43–50.
- ZAR, J.H. 1999. *Biostatistical analysis*. Upper Saddle River, NJ: Prentice-Hall, 663 pp.

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