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Environmental factors predicting the orientation of sea turtle hatchlings on a naturally lighted beach: A baseline for light-management goals

Shigetomo Hirama[a,b,*], Blair Witherington[c], Kristen Kneifl[d], Andrea Sylvia[a], Morgan Wideroff[e], Raymond Carthy[f]

[a] *Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1105 Southwest Williston Road, Gainesville, FL 32601, USA*
[b] *Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, P.O. Box 110430, Gainesville, FL 32611, USA*
[c] *Inwater Research Group Inc., 4160 Northeast Hyline Drive, Jensen Beach, FL 34957, USA*
[d] *Canaveral National Seashore, 212 South Washington Avenue, Titusville, FL 32796, USA*
[e] *Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 19100 Southeast Federal Highway, Tequesta, FL 33469, USA*
[f] *Florida Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, P.O. Box 110450, Gainesville, FL 32611, USA*

ABSTRACT

On sea turtle nesting beaches, artificial lighting associated with human development interferes with hatchling orientation from nest to sea. Although hatchling disorientation has been documented for many beaches, data that managers can use in understanding, predicting, and managing the issue are of limited detail. The present study provides baseline hatchling orientation data that can be compared to those from beaches with artificial lighting to prioritize light-management efforts there. In 2014, the precision of hatchling orientation was quantified for 87 nests on a naturally lighted beach that had little to no artificial lighting. Precision of hatchling orientation was regressed against seven environmental variables: beach slope, distance from nest to dune, dune height, apparent dune silhouette height relative to nest site, moon illumination percentage, cloud cover percentage, and relative humidity. Results favored a regression model that included distance from nest to dune, with shorter distances from the dune predicting a narrower angular range (i.e., greater precision) of hatchling orientation. The study confirmed findings of an earlier laboratory experiment that highlighted the importance to accurate hatchling orientation of a dark silhouette (dune) on the side of the nest site opposite the ocean side. Reducing artificial light and promoting the planting of pioneer plants that assist dune formation can increase hatchling survival.

1. Introduction

Natural lighting regimes are important regulators or facilitators of many aspects of animal behavior. Artificial lighting is a pollutant that threatens wildlife populations by altering natural ambient lighting in ways that modify the behavior of nocturnal animals (Venter et al., 2006; Falchi et al., 2016). The principal effect of light pollution on animal behavior is disruption of such behaviors as sleep, foraging, roosting, orientation, navigation, migration, dispersal, oviposition, mating, communication, and crypsis. This occurs in diverse taxa including marine worms, insects, fishes, amphibians, turtles, birds, and bats (Witherington, 1997; Longcore and Rich, 2004; Rich and Longcore, 2006; Raap et al., 2015; Stone et al., 2015). Behavioral disruptions can cause mortality directly in some species and can even alter population dynamics (Reed et al., 1985; Frank, 1988; De Groot, 1996).

Sea turtle behaviors can be altered by changes in ambient light regimes. For example, loggerhead turtles (*Caretta caretta*) have been shown to avoid nesting on lighted parts of a beach (Witherington, 1992). For hatchlings, artificial lighting 1) causes disorientation after emergence from nests in loggerheads and flatbacks (*Natator depressus*) (Salmon and Witherington, 1995; Kamrowski et al., 2014) and 2) slows and reduces directional swimming of loggerheads and green turtles (*Chelonia mydas*) hatchlings after they enter the ocean (Witherington and Bjorndal, 1991; Thums et al., 2016; Truscott et al., 2017). In the USA, artificial lighting has been identified as one of the most important mortality factors to mitigate for loggerheads, green turtles, hawksbills (*Eretmochelys imbricata*), Kemp's ridleys (*Lepidochelys kempii*), and leatherbacks (*Dermochelys coriacea*) (NMFS and USFWS, 1991, 1992, 1993, 2008; NMFS and USFWS, 2011). The majority of loggerhead nesting within the north-west Atlantic region occurs on Florida (USA) beaches (Ceriani and Meylan, 2017). To the extent that recovery of this species' populations is dependent upon nesting habitat quality, there is reason for concern. Florida has a high density of human development along the coast, with associated high levels of light pollution (Weishampel et al., 2016).

We conducted the present study to fill two information gaps that

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[*] Corresponding author at: Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1105 Southwest Williston Road, Gainesville, FL 32601, USA.

E-mail address: Tomo.Hirama@MyFWC.com (S. Hirama).

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impede managing the effects of artificial lighting on the orientation of loggerhead hatchlings. The first gap concerns defining what constitutes correct seaward orientation, that is, the pattern of orientation on beaches in which influences from artificial lighting are minimal, such as a natural beach. The first gap concerns orientation parameters that were collected at a naturally lighted beach, defining what constitutes correct seaward orientation. The second gap is a lack of knowledge of how environmental factors influence the hatchling orientation at a beach with no artificial lighting. As a result, no benchmark orientation–performance data exist that could be used as a goal in managing the light environment on sea turtle nesting beaches. Although some environmental factors are known to affect hatchling orientation in a beach with human development nearby (Limpus and Kamrowski, 2013), we found no field studies that correlated them with orientation parameters in no or little artificial light. By better understanding the importance of these variables, we can more effectively mitigate problems and thereby increase hatchling survival.

We proposed two principal research questions: 1) Do all hatchlings find and reach the sea with high orientation accuracy on a naturally lighted beach? and 2) Which environmental factors at loggerhead nest locations most strongly affect hatchling orientation? We collected hatchling-orientation data on a naturally lighted beach that was minimally affected by artificial lighting.

We evaluated the importance of seven environmental factors affecting hatchling orientation: beach slope (Salmon et al., 1992), distance from nest to dune, dune height – i.e., measurement of the vertical rise between the toe of the dune and the top of the dune vegetation (Mrosovsky, 1978; Salmon et al., 1992; Tuxbury and Salmon, 2005), apparent dune silhouette height – i.e., measurement of the vertical rise between the nest and the top of the dune vegetation, moon illumination (percentage) (Mrosovsky and Carr, 1967; Kamrowski et al., 2014), cloud cover (percentage) (Kyba et al., 2011; Jechow et al., 2017), and humidity (percentage) (Zieger et al., 2013; Fierz-Schmidhauser et al., 2010). We hypothesized that the precision of hatchling orientation would increase with increasing moon illumination, increasing cloud cover, increased humidity, increased dune height, increased apparent dune silhouette height, increased beach slope, and decreased distance from nest to dune. We were uncertain, however, as to the relative importance of each factor.

2. Methods

2.1. Study site

From July through September 2014 we collected data on hatchling orientation from 87 nests and measured associated environmental variables at the southern part of Playalinda (N28.77088°, W80.71956°–N28.64748°, W80.62646°), Brevard County, Florida, USA. The Playalinda section of Canaveral National Seashore is managed by the U.S. National Park Service. It has no lighted human development, and public access is prohibited after sunset. Thus, it is one of the Florida beaches least affected by artificial light and is described as a natural coastal system (Antworth et al., 2006) or completely natural beach (Erb and Wyneken, 2019). The closest source of artificial light is the city of Titusville, about 18 km west of the study area, with inconspicuous sky glow reaching the beach, based on our observations. The light intensity data that were measured using a Sky Quality Meter (Unihedron, SQM-L) along with photographic images showed the present study site has minimal impact from artificial lighting (https://hoiprediction.shinyapps.io/hatchling/, where CNS indicates Playalinda). The beach's dune vegetation is dominated by native sea grape (*Coccoloba uvifera*) and sea oats (*Uniola paniculata*), which are not trimmed and so increase the height of the dune's silhouette, which blocks ambient light. Beach nourishment (replenishment of sand), the use of sandbags to retard beach erosion, mechanical beach cleaning, and dune reconstruction, all of which can modify beach profiles (wide and flat) and are common at other Florida beaches, have never been done at Playalinda.

2.2. Hatchling orientation precision (angular range) and accuracy (modal divergence)

In approximately two-hour surveys conducted after sunrise, we recorded bearings of hatchling tracks at nests that showed track evidence from at least five individuals (Pendoley, 2005). Following methods from Salmon and Witherington (1995), we collected bearings with a sighting compass at each track's intersection with a circle that had a radius of 10 m (testing circle) and its center at the middle of the nest (Fig. 1). We collected three orientation parameters: 1) the angular range, which indicates precision (i.e., the spread of hatchling tracks as indicated by bearings at the widest parts of the tracks on a test circle; Fig. 1); 2) modal divergence (the difference between the most frequent direction, or mode, in which hatchlings crawled and the most direct path to the ocean, which shows accuracy; Fig. 1); and 3) number of circlers (i.e., hatchlings whose tracks made at least one complete circle). For each emergence, we assigned four categories for the number of circlers: 0, 1, 2, and 3+. Although it is possible (but unlikely) that some of the orientation-measure replicates (nests) could have been from the same female turtle, we find no evidence that the behavior of hatchlings would have a consequential genetic-relatedness component in comparison to environmental factors.

2.3. Ecological data

We selected environmental variables that have been shown to influence sea turtle hatchling orientation, based on our knowledge and the literature. These variables were beach slope, distance from nest to dune, dune height, apparent dune silhouette height, moon illumination, cloud cover, and humidity. Immediately after collecting orientation data, we measured or gathered data on environmental variables as follows: 1) for beach slope, we used an inclinometer set on a 1-m length board placed immediately seaward of the nest (emergence point); 2) for distance from nest to dune, we used a tape to measure to the vegetation line that approximates toe of dune; 3) for dune height including vegetation, we used an inclinometer and a measuring tape; 4) for apparent dune silhouette height, we measured from the nest, the angle of inclination to the top of dune vegetation; 5) for moon illumination, we obtained data for the emergence date using the R package "lunar" that contains lunar information (Lazaridis, 2015; R Core Team, 2017); 6) average of humidity percentage overnight (humidity), and 7) for cloud cover, we extracted data (humidity and cloud cover) for nest locations with a spatial resolution of 2.5° latitude and longitude (Kemp et al., 2011) from the National Oceanic and Atmospheric Administration's climate data (Earth System Research Laboratory, Physical Sciences Division) by using the "RNCEP" package for program R (Kalnay et al., 1996). These environmental variables were then regressed against the angular range of hatchling tracks. We did not use modal divergence because we found this measure at Playalinda to vary little across environmental factors.

We measured dune height from the seaward dune vegetation line, which was undisturbed at Playalinda and reliably located at the toe of the dune. We felt that this direct, high resolution and contemporaneous measure represented local environmental conditions better than digital elevation models or Light Detection and Ranging data.

2.4. Statistical analyses

We used program R (version 3.3.1) with relevant packages to conduct all data analyses. We ran circular analyses to test the modal hatchling and ocean directional distributions for circular uniformity using Rayleigh tests (Pewsey et al., 2013) with the "circular" R package (Lund et al., 2017). For checking normality of the data, we examined distributions of each parameter followed by running Shapiro–Wilk normality tests. By using either a parametric or nonparametric

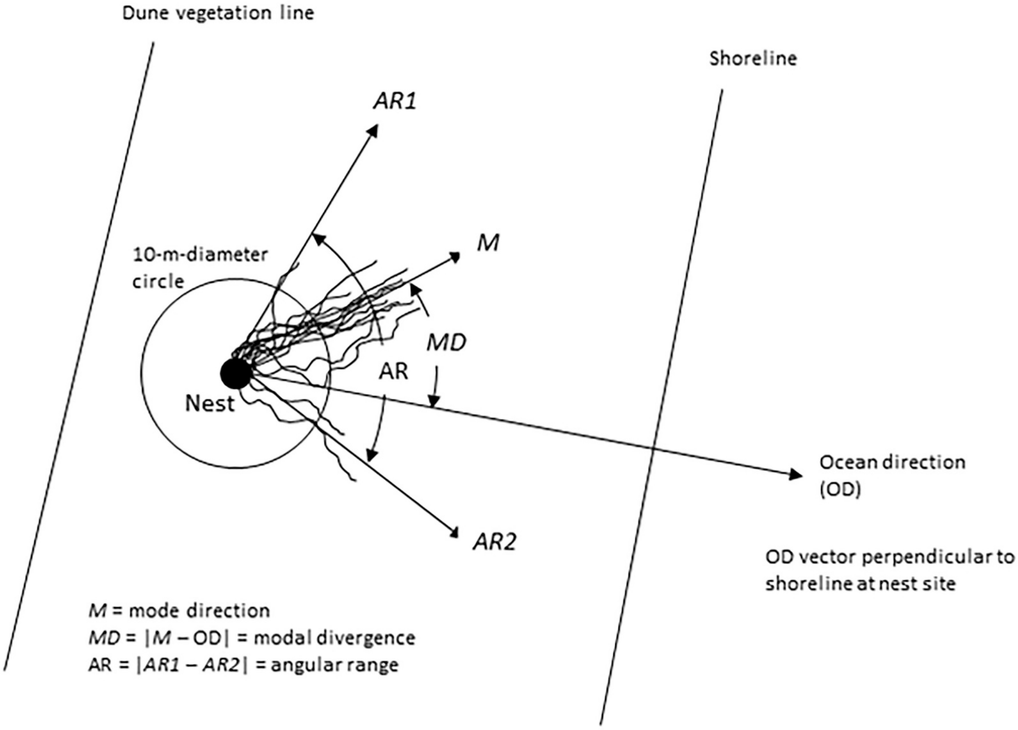

Fig. 1. Two parameters, angular range (absolute value of AR1 − AR2) and modal divergence (absolute value of M − OD), were used to describe sea turtle hatchling orientation accuracy for Playalinda, Florida. Measurements were taken where hatchling tracks intersected with a 10-m-diameter circle centered on the nest.

correlation test, depending on normality, the relationships between angular range of each nest and the seven environmental parameters were examined. We used multiple linear regression to determine the best combination of environmental factors describing angular range, where angular range of an individual nest was treated as the dependent variable, and environmental variables were treated as the independent variables. We included all additive effects of environmental variables, as well as a three-way interaction of moon illumination percentage, cloud cover percentage, and percent humidity, to account for possible celestial and weather-related interactions affecting angular range of sea turtle hatchlings. In our evaluation of collinearity of environmental data, if a variance inflation factor was >5, the variable was considered to have similar effects as at least one other variable (Gill, 1986) and was removed from further analyses. Candidate model residual plots were assessed for violations of model assumptions, and automated stepwise model selection (reduction) (Mazerolle and Linden, 2019) was used to find the most strongly supported model using Akaike's information criterion (AIC), where the lowest AIC score represents the most parsimonious model (Akaike, 1973). All significance levels were chosen as 0.05.

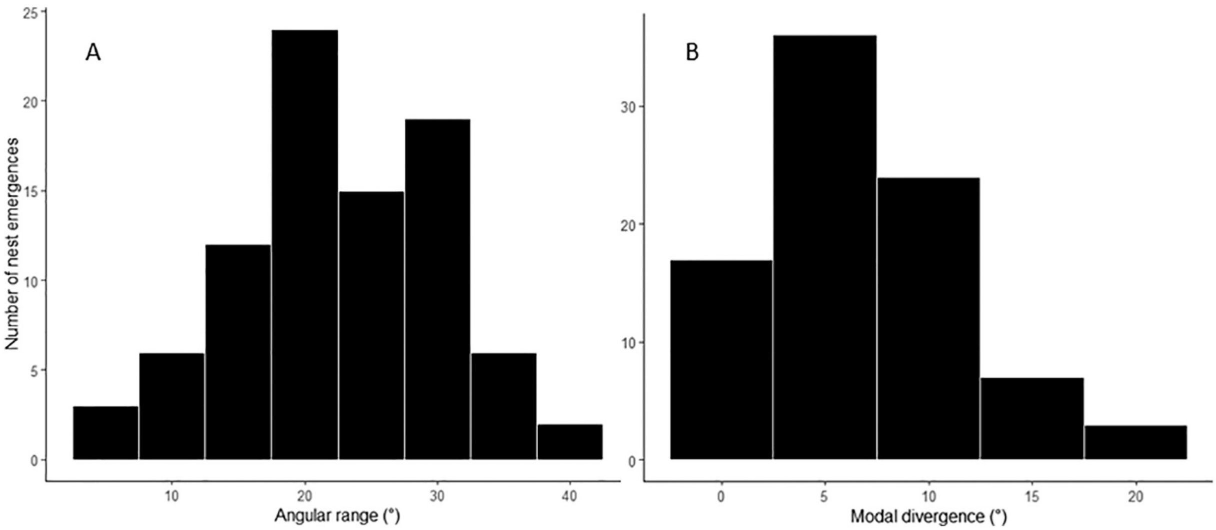

Fig. 2. Angular range (A: n = 87, mean = 23.6°, median = 22.5°, range = 5–40°, standard deviation = ± 7.8°) and modal divergence from ocean direction (B: *n* = 87, mean = 7.4°, median = 6.3°, range = 0–21.3°, standard deviation = ± 4.9°) of loggerhead hatchling tracks from Playalinda, Florida.

3. Results

3.1. Hatchling orientation precision and accuracy

The results of angular range and modal divergence from 87 clutches provided baseline orientation precision and accuracy data for a naturally lighted beach (Fig. 2). The result of the Rayleigh test for hatchling orientation revealed which mode directions differed significantly from random mode direction (test statistic$_{85}$ = 0.9948, $p < 0.0001$), meaning that hatchlings oriented to a specific direction within the testing circle (Fig. 3). The mean mode and ocean directions were 56.5° (SD ± 0.12°) and 59.3° (SD ± 0.06°) (Fig. 3). All tracks between nest and sea were relatively straight; none of the emerging hatchlings were circlers.

3.2. Modeling angular range against ecological variables

For creating predictive models, we correlated angular range against environmental variables (Table 1). The angular range parameter showed a wider range of values than did modal divergence, possibly as a response to the environmental variables, and therefore was effective to use in modeling. As a result of the normality tests along with examining data distributions, we chose Spearman's rank correlation tests (nonparametric) to examine the relationships between angular range and seven environmental parameters. The results of the correlation tests showed that angular range was significantly correlated with three parameters, distance from nest to dune ($p = 0.007$, ρ (correlation coefficient) = 0.312) (Fig. 4), cloud cover ($p = 0.006$, $\rho = -0.289$), and apparent dune silhouette height ($p = 0.001$, $\rho = -0.375$) and was weakly correlated with moon illumination ($p = 0.099$, $\rho = -0.176$). The remaining parameters, beach slope ($p = 0.504$, $\rho = 0.125$), dune height ($p = 0.880$, $\rho = -0.017$), and humidity ($p = 0.839$, $\rho = 0.022$) indicated no significant correlations.

We confirmed that multicollinearity across the seven environmental variables was below the threshold, with all variance inflation factor scores < 5: 1.09 (beach slope), 2.91 (distance from nest to dune), 1.45 (dune height), 2.00 (humidity), 2.08 (cloud cover), 3.52 (moon illumination), and 2.71 (apparent dune silhouette height). Candidate model residual plots showed linear, randomly spread, and normally distributed patterns. The best-supported multiple-regression model describing hatchling orientation retained one covariate, distance from nest to dune (ΔAIC = 0.00, Wi = 0.38; Table 2; Fig. 4).

For our naturally lighted beach, we suggest that the best linear regression model describing angular range is:

linear model $_{\text{angular range}}$ = 22.33 + (distance from nest to dune) ×

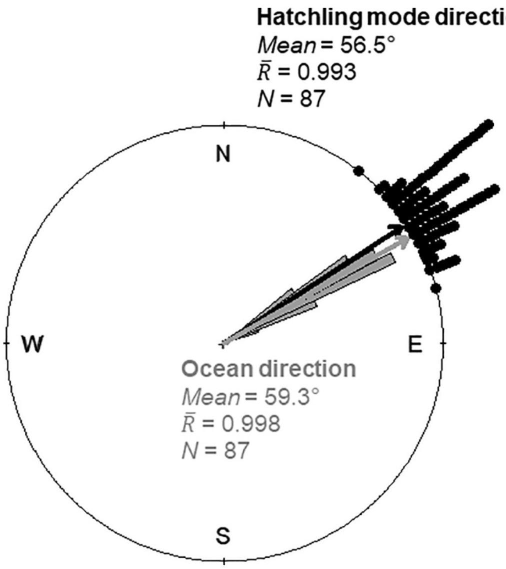

Fig. 3. The stacked black dots outside of the circle show the mode directions (the most frequent directions in which hatchlings crawled) of loggerhead hatchling tracks in Playalinda, Florida. The rose diagram inside the circle indicates the direction of the ocean relative to each nest. The black and gray arrows show the means of hatchling mode and ocean directions. *Mean* indicates the mean values of mode orientation bearings of 87 nest emergences and ocean directions relative to the emergence point. *Rbar* indicates how close sample modes are to mean direction; it becomes 1 only when all of directions are stacked at one point (Pewsey et al., 2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary statistics of ecological variables for Playalinda, Florida. SD indicates standard deviation of means of variables, Range represents the max-min of the data, maximum and minimum values are inside brackets, CV represents the coefficient of variation of the variables, VM represents the percent variation of the range from the mean calculated as $\frac{Mean}{Max - Min} \times 100$.

Ecological variables	Mean	SD	Range [min, max)	CV	VM
Beach slope (°)	9.68	±5.12	26.80 [−6.60, 20.20]	52.89%	276.86%
Dune height (m)	3.42	±1.44	5.32 [1.30, 6.62]	42.11%	155.56%
Distance from nest to dune (m)	2.14	±2.75	11.95 [−3.85, 8.10]	128.50%	558.41%
Humidity (%)	90.57	±3.59	11.89 [83.81, 95.70]	3.96%	13.13%
Moon illumination (%)	58.62	±26.46	85.30 [14.00, 99.30]	45.14%	145.51%
Cloud cover (%)	52.89	±10.88	33.32 [39.79, 73.11]	20.57%	63.00%
Apparent dune silhouette height (°)	21.27	±13.06	76.02 [4.98, 81.00]	61.40%	357.40%

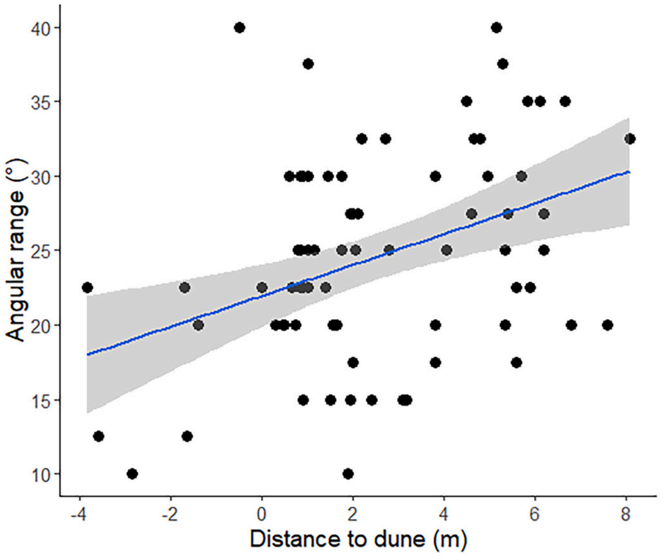

Fig. 4. Scatterplot of the top linear regression model (determined by Akaike's information criterion) showing the orientation accuracy (angular range as response variable) of loggerhead hatchlings with the distance between nest and dune (distance to dune) as the explanatory variable at Playalinda, Florida [$y = 22.33 + 0.94$ x (distance to dune), $r^2 = 0.12$, p = 0.001]. The shaded area shows the 95% confidence interval for predictions of the linear model.

Table 2

The results of automated stepwise model selection with AIC_c. Effects evaluated at Playalinda, Florida include: the distance between a nest and the dune vegetation line that is at the toe of the dune (dune distance); moon illumination percentage (moon); apparent dune height including height of vegetation (dune height); average of humidity percentage overnight (humidity); dune silhouette height relative to nest (silhouette height); cloud cover percentage over the study area (cloud); beach slope that is seaward of emergence location (slope); three-way and two-way interactions between moon illumination percentage, humidity, and cloud cover percentage. Parameters in the table include AIC_c = Akaike's information criterion for small sample size; ΔAIC_c = AIC of the model less the AIC of the top model; W_i = Akaike weight; and K = number of parameters.

Model description	AIC_c	ΔAIC_c	W_i	K
Angular range ~ dune distance	278.75	0.00	0.38	2
Angular range ~ dune distance + moon	279.13	0.38	0.31	3
Angular range ~ dune distance + moon + humidity	280.30	1.55	0.18	4
Angular range ~ dune distance + moon + humidity + cloud	282.12	3.37	0.07	5
Angular range ~ dune distance + moon + humidity + cloud + humidity*cloud	283.74	4.99	0.03	6
Angular range ~ dune distance + moon + humidity + cloud + moon*cloud + humidity*cloud	285.11	6.36	0.02	7
Angular range ~ dune distance + moon + humidity + cloud + moon*cloud + humidity*cloud + humidity*moon	286.73	7.98	0.01	8
Angular range ~ dune distance + moon + humidity + cloud + slope + moon*cloud + humidity*cloud + humidity*moon	288.38	9.63	0.00	9
Angular range ~ dune distance + moon + humidity + cloud + slope + moon*cloud + humidity*cloud + humidity*moon + humidity*moon*cloud	290.04	11.29	0.00	10
Angular range ~ dune distance + moon + humidity + cloud + slope + silhouette height + moon*cloud + humidity*cloud + humidity*moon + humidity*moon*cloud	291.84	13.09	0.00	11

0.94.

The standard errors of the intercept and the distance to dune were ± 1.04 and ± 0.29, respectively. The variance explained by the model was statistically significant ($F_{1,72} = 10.76$, $p = 0.002$), the two independent variables describing 12% of the variance in angular range. Angular range increased with distance to the dune ($t = 3.28$, $p = 0.002$).

4. Discussion

4.1. Expectation of hatchling orientation accuracy and precision on a naturally lighted beach

Hatchling orientation data representing a naturally accreted, vegetated, and nonlighted beach are rare, largely because geographical expansion of human development and associated artificial lighting have limited availability of these beaches. Our study area was relatively distant from human development, making it one of the ideal locations to establish baselines of hatchling orientation parameters. Among the studies that used the same orientation parameters as the present study, some had different numbers of hatchling tracks included in the data set; not indicated for loggerhead (Salmon and Witherington, 1995), twenty for flatback (Kamrowski et al., 2014), ten for loggerhead (Berry et al., 2013) hatchlings, implying there is uncertainty of the representative track numbers used. In the present study, we included nest emergences that had five or more tracks, based on a previous study of loggerhead hatchlings (Pendoley, 2005). The results of the present study showed high accuracy and precision of hatchling orientation toward the sea, as we predicted for a naturally lighted beach. Previous work considered hatchling orientation to be disrupted when angular range exceeded 90° or modal divergence exceeded 30° (Salmon and Witherington, 1995). When those criteria were applied in the present study, no orientation was disrupted, although such disruptions are common on most Florida nesting beaches (Salmon and Witherington, 1995). Under the most challenging environmental conditions for hatchling orientation at Playalinda (20 m between nest and dune), our model predicted that hatchlings would orient relatively well, with an angular range of 46.6° [linear model $_{\text{angular range}} = 22.33 + 20 \times (0.94) = 48.06°$]. As a caveat, it is clear that some associated factors were not captured in the covariates that influenced angular range, given that about 12% of the variance was explained in the model. Environmental conditions not measured in the present study included wave height and wind variables, which could influence surf sound or turbulence-related surf reflection. We did not test hypotheses for these variables because there was no support in the literature nor personal observations suggesting that these variables contributed as important orientation cues. In the present study, we observed the tracks in sand that were left by naturally emerged hatchlings. A similar study could be done using arena assay tests releasing hatchlings in a more controlled setting over the factors. We also did not test for the possibility that the number of hatchlings in an emergence event might affect individual orientation. Do hatchlings follow their siblings or avoid their paths after emerging from a nest? Although our personal observations suggest no such variation between hatchlings orienting as a group or as individuals, we suggest that the topic merits study.

Evaluating other loggerhead nesting beaches against baseline hatchling orientation parameters from the present study would help manage these nesting beaches. We expect that many beaches where managers believe emerging hatchlings are unaffected by artificial lighting may actually show significant orientation differences against the baselines we present here. Hatchlings in the present study showed better orientation (in both angular range and modal divergence) than did hatchlings studied on beaches on the Greek island of Zakynthos (Dimitriadis et al., 2018) and on Australia's Woongarra coast (Berry et al., 2013), both of which were located in conservation areas but near human development. We suggest that the loggerhead hatchling emergence parameters we measured could be used to assess seaward orientation accuracy throughout the loggerhead's global range. Conducting additional similar studies at beaches with natural light environments but with differing beach-slope and dune attributes might expand our understanding of hatchling orientation-accuracy baselines. Our results highlight the need for beach-specific orientation data that could be compared to a catalog of data from other beaches. These assessments would provide a measure of the extent to which managers could make improvements in light management to increase hatchling survivorship.

4.2. Two environmental factors that affected hatchling orientation

In the present study, hatchling orientation was more precise at shorter distances from nest to dune. Laboratory experiments have shown that a dark silhouette, a visual cue, was a more important orientation cue than was slope, a gravitational cue (Salmon et al., 1992). In another laboratory experiment, artificial silhouettes and controlled light levels, simulating the beach dune and varying intensities of lunar illumination, interacted and impacted hatchling orientation (Tuxbury and Salmon, 2005). Therefore, we predicted that a dark silhouette opposite the nest from the sea would be an influential cue and that orientation would improve as the distance between the nest and dune decreased. Our model confirmed this prediction, and the parameter, distance from nest to dune, was the best predictor of the seven environmental variables. We should point out that two other models, which included 1) distance from nest to dune and moon illumination and 2) those variables as well as percent humidity, had ΔAICs of <2, indicating that there was support for other covariates in the stepwise procedure. But our results support the hypothesis that dune silhouette, specifically its apparent height and other factors increasingly discernible with proximity, such as dune shape, has the greatest influence among the variables we measured on hatchling orientation at a naturally dark beach.

4.3. Influence of other environmental factors on hatchling orientation

At Playalinda, apparent dune silhouette height and orientation precision (angular range) did not show a significant relationship (Table 2), contradicting results of laboratory experiments that found silhouette height to serve a critical role in hatchling orientation toward the ocean (Salmon et al., 1992). We hypothesize that the relatively uniform and well-established dune at Playalinda did not provide variation in apparent dune silhouette height that would have significantly affected orientation precision. The silhouette-height threshold appears to be lower than the approximately 30° vertical height over which hatchlings may assess field brightness (Table 1 in the present study, Lohmann et al., 1997). Although we found no significant silhouette-height effect on our dark study beach, on beaches that are exposed to light pollution, dune height might have an important influence on hatchling orientation because it would block some of the artificial light.

We find it noteworthy that, independent of silhouette height, orientation precision was reduced (i.e., angular spread of tracks increased) with increasing distance between nest and dune (Table 2). We hypothesize that this is an effect of visually discerned dune structure. Because hatchlings are likely to be myopic on land (Ehrenfeld and Koch, 1967), their ability to use form vision to perceive distant shapes may be limited. Additional studies of orientation effects among factors including dune height, dune structure, and distance from these potential cues would help clarify the integration of these sensory inputs. The effectiveness of dune height in reducing orientation effects from artificial lighting on heavily light-polluted beaches can be evaluated, given that a dune height is possibly more important for better hatchling orientation by blocking the light. A taller, more densely vegetated dune can also be evaluated as an additional data input to management decisions for mitigating detrimental effects on hatchling orientation where beach nourishment has artificially widened the beach and resulted in turtles nesting further from the dune.

Greater moon illumination helped increase orientation precision, although the contribution was weak and not worth including in the best predictive model. Moon illumination was included as a factor in two models that showed a ΔAIC of <2. We expected that moon illumination would be a crucial predictor of hatchling orientation. During a full-moon night, not only the illumination percentage, but also the duration of moon visibility in the night sky, is at a maximum, because the moon is located opposite the sun and rises as the sun sets. As the moon wanes, both illumination percentage and visible duration in sky decrease. This would accentuate the relative effect of moonlight. In a study at Tortuguero, Costa Rica, orientation accuracy of green turtle (*Chelonia mydas*) hatchlings increased as the moon illumination increased (Mrosovsky and Carr, 1967). On beaches that have coastal development, moon phase affected accuracy of orientation; hatchling disorientation was recorded at more nests around the new moon and at fewer nests around the full moon (loggerheads in Salmon and Witherington, 1995, and Berry et al., 2013; flatback sea turtles in Kamrowski et al., 2014). By adding ambient light and creating fewer artificially anisotropic (highly directed) light fields, moon illumination percentage might have more influence on hatchling orientation on developed beaches than on a naturally lighted beach like Playalinda. Along with dune height, we suggest that moon illumination be investigated further to determine whether our findings can be applied to beaches with greater levels of light pollution.

Humidity correlated minimally with orientation precision. We had predicted that high humidity could manifest as saltwater aerosols that would magnify light intensity by reflecting and diffusing light. Additional study of this environmental factor could include more direct measurement of aerosols or of the wave action that produces it.

Slope, which can affect tactile (i.e., gravitational) and visual cues, did not affect hatchling orientation accuracy. A gravitational cue has its effect as a turtle crawls from a higher to lower elevation; a visual cue has its effect by obstructing a clear view of the ocean as a turtle crawls from the emergence location toward the ocean. In either case, gravity or visual, beach slope had no significant measured effect on orientation in the present study. Slope assisted the orientation of hatchlings via gravity only when light cues were absent in a laboratory experiment (Salmon et al., 1992); gravity was found to be less important than phototropotaxis in earlier work (Mrosovsky and Shettleworth, 1968). In the present study, a few nests that were deposited in the dune had a positive slope (uphill) toward the ocean such that hatchlings had no clear view of water, yet they still showed accurate seaward orientation. At Tortuguero, green turtle hatchlings were observed to orient correctly without a direct view of the ocean (Ehrenfeld and Carr, 1967). In the present study, we measured slope across one-meter seaward of each nest. Our rationale was that the first meter of travel was critical, because a hatchling perceives orientation cues immediately after emerging from sand and because the majority of track-direction changes we have observed occur in this first meter. Although the beach slope changed across the 10-m radius site within which orientation accuracy was measured, we did not see substantial changes in track direction between the one-meter and 10-m radius. The results of the present study indicate that slope steepness and direct view of ocean were not critical for successful orientation; instead, the general contrast of light—darker toward the dune and brighter toward the sea—might have assisted turtles in crawling seaward.

5. Conclusions and management implications

We suggest that our undeveloped Florida study beach, with its naturally steep beach profile, prominent dune, and absence of artificial light, was ideal for effective hatchling orientation. Many beaches are likely to depart from this ideal condition. To understand the consequences of orientation environments at sea turtle nesting beaches, we suggest collecting hatchling orientation data following this and past studies (Salmon and Witherington, 1995; Pendoley, 2005; Berry et al., 2013; Kamrowski et al., 2014). Results of hatchling orientation that significantly differ from representative baselines may indicate the need to restore the beach environment, and especially, to reduce visible artificial lighting. Coastal construction and other human activities that impact the beach–dune system can be managed in a way that minimizes change in natural beach profiles, including beach width, that can alter nest placement relative to the dune. Beach nourishment commonly creates a beach that has a wide, flat profile, and, as a consequence, turtles often nest farther from the dune (Brock et al., 2009; Jackson et al., 2010). At greater distances between dune and nest, the success of seaward orientation is likely to decrease because a dune's silhouette is reduced relative to the expanse of ocean horizon. Moreover, when a beach is nourished, the area used for nesting is elevated, and nearby artificial lighting that had been blocked by the dune often becomes more evident (Brock et al., 2009). Beach-nourishment projects that strive to create or restore dune and beach profiles like those of a naturally lighted beach may reduce disruptions in hatchling orientation. Additional actions designed to minimize impacts from beach nourishment include revegetating dunes with diverse native species that include pioneering plants on the dune face and taller, woody plants where they would be distributed in a mature natural dune system (Cheplick, 2006). This, coupled with strenuous management of artificial light sources near the beach, may assist successful sea finding and greater hatchling success on all nesting beaches.

CRediT authorship contribution statement

Shigetomo Hirama: Conceptualization, Funding acquisition, Investigation, Methodology, Data curation, Writing- original draft & final editing. **Blair Witherington:** Methodology, Writing - review & editing. **Kristen Kneifl:** Supervision, Writing - review & editing. **Andrea Sylvia:** Formal analysis, Writing - review & editing. **Morgan Wideroff:** Data curation, Writing - review & editing. **Raymond Carthy:** Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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