Direct and indirect pathways for environmental drivers of hatching success in the loggerhead sea turtle

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ABSTRACT: Nest site selection has consequences for hatching success by mediating the temperature and moisture conditions that eggs experience during the incubation period. Understanding the potentially complex pathways by which nest placement influences these abiotic mediators, and therefore hatching success, is important for predicting which nests will be successful and which may require management action. We studied the effects of loggerhead sea turtle (*Caretta caretta*) nest site selection on hatching success by linking nest placement characteristics to hatching success through a structural equation model. We monitored 170 nests on Ossabaw Island, Georgia, during the summers of 2017 and 2018 and tracked nest conditions throughout the incubation period. Temperature had a complex effect on hatching success — nests had higher hatching rates if they were exposed to higher mean temperatures but also if they experienced both extremely high (>34°C) and extremely low (<26.5°C) temperatures, suggesting that temperature variability plays a role in determining nest outcomes beyond the mean temperature. Likewise, hatching success declined with a higher incidence of nests being inundated by tides. We found that nests placed at the highest elevations had the highest hatching success rates, likely because those nests had a much lower chance of being washed over by high tides and had higher mean temperatures. Nests were also more successful when placed in greater amounts of vegetation, again because vegetated nests were generally warmer and were associated with fewer washover events. These results shed light on the mechanisms behind selection for certain nest site characteristics and can guide the relocation of nests as a conservation action.

KEY WORDS: Loggerhead sea turtle · Hatching success · Environmental drivers · Structural equation modeling

1. INTRODUCTION

For species that lay their eggs in enclosed environments, such as in the ground or in cavities, nest site selection determines the abiotic environment (e.g. temperature and moisture) in which eggs will develop. Temperature and moisture conditions have a strong influence on hatching success across taxonomic groups, with most species having thermal and moisture optima that result in the highest hatching success (Spotila et al. 1994, Butler et al. 2009, Du &

Shine 2015). However, the relationship between the habitat features that a nesting female uses to select a nest site (e.g. density of surrounding vegetation) and temperature and moisture may be complex. For instance, nest characteristics such as depth and surrounding vegetation density can interact to influence nest temperature mean and variability in different ways (Shine & Harlow 1996, Morjan 2003). This complexity makes predicting how nest site characteristics will influence hatching success challenging, and such predictions are important for species that may

be undergoing declines in hatching success due to changes in their environments.

Many sea turtle populations around the world are experiencing nest hatching success challenges due to increases in temperature (Laloë et al. 2017), sea level rise (Fuentes et al. 2011), increases in predator populations (Brost et al. 2015), and negative consequences of beach development (Siqueira et al. 2021). Often, sea turtle nests are relocated to different areas of a beach to try to improve hatching success (Tuttle & Rostal 2010, Ilgaz et al. 2011) since the egg stage for sea turtles is considered especially vulnerable (Özdemir et al. 2008) and is also the easiest life stage to manage. Several environmental and biological factors can determine whether eggs laid in a nest on the beach ultimately emerge as hatchlings or fail; such factors include temperature, moisture, elevation, sand characteristics, inundation, predation, and poaching (Foley et al. 2006, Tomillo et al. 2008, Butler et al. 2020). For nest relocation strategies to be most successful, a more complete understanding and predictive framework for environmental parameters on hatching success is required.

Temperature is among the most important environmental drivers of hatching success in sea turtles, where suitable temperature for incubation typically falls in a relatively narrow range of temperatures (Bull 1980, Yntema & Mrosovsky 1982, Blair 2005). When incubation temperatures fall outside of the suitable range, lower hatching success and/or complete nest mortality can occur. Many nests within current sea turtle nesting ranges will be exposed to temperatures that exceed the suitable temperatures within years or decades (Butt et al. 2016). High nest moisture can delay development, increase mortality, and impede hatchling emergence (Marco et al. 2017), while low nest moisture can lead to desiccation (McGehee 1990), although impacts of moisture are variable (Wood & Bjorndal 2000, Foley et al. 2006, Lolavar & Wyneken 2015) and potentially interact with nest temperature (Godfrey et al. 1996). Finally, tidal washover and prolonged nest inundation decrease hatching success due to embryo asphyxiation (Wood & Bjorndal 2000, Foley et al. 2006), particularly when the frequency and intensity is high, and inundations occur during critical incubation periods (Limpus et al. 2020).

While temperature, moisture, and tidal washover are considered important drivers of hatching success, several other nest characteristics can influence any of these drivers, necessitating *in situ* observations of multiple parameters. For example, nests at higher elevations can have suitable temperatures (Pfaller et al. 2009) while decreasing the number and duration of inundations. However, nests at high elevations may result in temperatures that are too high and moisture levels that are too low (Lolavar & Wyneken 2015, Hays et al. 2017, Kobayashi et al. 2017). Although elevation may serve as a major cue for nest location in sea turtles (Wood & Bjorndal 2000), the multiple pathways through which elevation influences temperature and moisture require further attention. Likewise, vegetation could impact nest variables by shading, minimizing heat transfer, and/or creating a drying effect from transpiration (Fowler 1979, Ferreira Júnior et al. 2008), although the overall impacts of vegetation are mixed (Serafini et al. 2009, Ditmer & Stapleton 2012, Kamel 2013). Some sea turtles may use the presence of vegetation as an indicator of nesting habitat (Fujisaki et al. 2018), although vegetation could also impede nesting (Hays & Speakman 1993). Finally, dune morphology might affect nest environments as the sun strikes nest sites at different angles, with varied radiation intensities, and for varying times per day (Maurer & Johnson 2017). The dip (slope relative to a horizontal plane) of the seaside (generally the windward side) portion of a dune could also impact incubation conditions, as the steepness of the dune can potentially impact heating during the day and drainage after inundation or precipitation (Berndtsson et al. 1996).

Loggerhead sea turtles *Caretta caretta* may be an ideal species to examine the complex interactions between nest site parameters and the environmental drivers of hatching success. The loggerhead is federally listed as a threatened species, and there is considerable research on numerous variables that influence loggerhead hatching success with aims to improve conservation and management strategies (e.g. Foley et al. 2006, Ditmer & Stapleton 2012, Lolavar & Wyneken 2021). However, it is currently unclear which environmental factor, combinations of factors, or interactions between factors may have the greatest impact on hatching. Given that current conservation strategies incorporate nest relocation, which incurs considerable labor costs and resources, improved information on nest parameters may lead to increased success and efficiency of nest relocation programs. Further, the factors that currently limit hatch success are likely to be exacerbated under future climate conditions, with potentially warmer sand temperatures, alterations in precipitation patterns, and changes to dune vegetation (Feagin et al. 2010) as well as erosional loss of beaches with sea level rise (Griffin & Henry 1984, Meyer 2013). By building a predictive framework which links multiple

factors to loggerhead sea turtle hatching success, it is possible to update management protocols to increase efficiency in conservation efforts by concentrating relocation efforts only on high-risk nests and selecting optimal sites when relocation is necessary.

Therefore, our main objective was to explore how a combination of environmental parameters (temperature, moisture, and tidal inundation) and the nest characteristics that affect those parameters (vegetation, elevation, distance from the tideline, and dune morphology) may interact to affect hatching success in loggerhead sea turtle nests on a barrier island. We collected environmental variables for 170 nests across 2 nesting seasons on Ossabaw Island, Georgia, USA.

2. MATERIALS AND METHODS

2.1. Study site

Sea turtle nest monitoring was conducted on Ossabaw Island, Georgia, USA. Ossabaw is Georgia's third largest barrier island (31.77° N, 81.08° W; Fig. 1). The climate on Ossabaw is categorized as humid subtropical, with generally hot summers and mild winters. Ossabaw Island is managed by the Georgia Department of Natural Resources (DNR) and is only accessible by boat with very limited public access and remains relatively undeveloped with 9000 acres
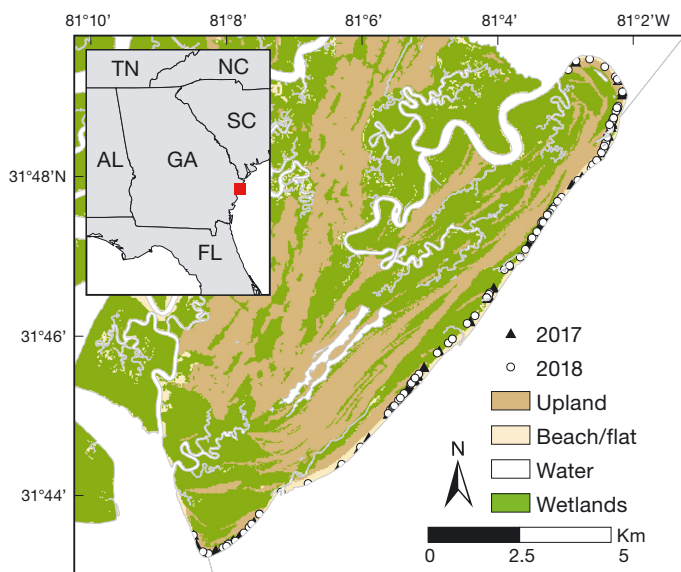

Fig. 1. Loggerhead sea turtle nest locations on Ossabaw Island, Georgia, from 2017 (black triangles) and 2018 (white circles). Black lines indicate locations of tidal channels that separate the 5 beaches on the island. Land cover data are from the 2016 National Land Cover Database. Main map location is indicated by the red square in the inset

(3642 ha) of upland habitats beyond tidal influence and 16 000 acres (6475 ha) of marshland intersected with tidal creeks. The island's oceanside coast consists of 5 beaches, separated by small tidal creeks, which total ~17 km for potential sea turtle nesting habitat. The beaches include North Beach (~7 km), North Middle (~2 km), Middle Middle (~1 km), South Middle (~5 km), and South Beach (~2 km; Fig. 1). No human-made structures such as sea walls obstruct sea turtle access to these beaches. Further, due to limited accessibility, there is little direct human impact to turtle nests.

2.2. Nest excavation, inventories, and monitoring

All beaches on Ossabaw Island were monitored daily during Georgia's nesting season (5 May–8 Sep 2017, 3 May–26 Sep 2018) beginning at first daylight, approximately 30 min before sunrise. Sampling was shortened in 2017 due to Hurricane Irma. Every morning, new nests were located by observation of turtle tracks in the sand culminating in the presence of a body pit, thrown sand, and often disturbed vegetation. The body pit was probed with a stick to locate the egg chamber. When an egg chamber was located, sand was removed from the top of the chamber, eggs were carefully removed and counted, egg chamber depth (to the bottom of the chamber) was measured, and eggs were returned to the nest. When half of the eggs were returned, a HOBO Pendant temperature data logger[1] (accuracy ±0.53°C) set to record temperature at 30 min intervals attached to a nylon mason line was placed into the middle of the nest approximately halfway from all sides of the nest chamber. The remaining eggs were returned to the nest, and the eggs were re-covered with sand. Egg removal occurred between 06:20 and 10:30 h (except for 10 nests which were discovered when beach monitoring lasted beyond 11:00 h). In total, eggs were kept out of the chamber for no more than 5 min before being replaced. When eggs are removed within 12 h of oviposition, it is generally considered to do little harm because the embryo has not yet broken from pre-ovipositional embryonic arrest and attached to the wall of the egg (Williamson et al. 2017). After initial inventory, nests were covered with a 1.2 × 1.2 m plastic screen (5.5 cm diamond mesh) staked down at the 4 corners with a metal

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[1]Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

pencil rod to deter potential predators but allow hatchlings to exit the nest. For the first 45 d, an additional 0.6 × 0.6 m hardware cloth (15 mm diamond mesh) was centered over the nest to prevent raccoons *Procyon lotor* and ghost crabs *Ocypode quadrata* from entering the nest. This small mesh was removed at 45 d to prevent emerging hatchlings from becoming trapped. Nests were monitored and maintained following Georgia DNR protocols, and fieldwork methods were approved by the Institutional Animal Care and Use Committee (IACUC) of Georgia Southern University (No. I17009).

Due to logistics, we could not monitor nest site characteristics for every nest laid on Ossabaw Island during our survey seasons. However, we attempted to select nest sites in proportion to the overall population of nests on each of the 5 beaches (i.e. if 50 % of island nests were located on North Beach, approximately 50 % of the selected sample were North Beach nests). Based on Ossabaw nesting history from 2012 to 2016 nesting seasons (Georgia DNR, seaturtle.org), on average 47 % of total nests for the island are deposited during the month of June, so approximately 47 % of the sampled population were nests deposited in June. The same methodology was applied for all other months in the nesting seasons.

For the duration of the nest incubation, nests were visually inspected daily. Tidal washovers were recorded daily, and any incidence of predation was noted; predator screens were maintained following Georgia DNR protocols. Nests were inspected and maintained daily until predation occurred, hatchling tracks were found, or 70 d after the nest was deposited. Once hatchling tracks were observed leaving a nest, the nest was marked as hatched, and the nest was inventoried 5 d later. If no signs of hatchlings were observed after 70 d of incubation, the nest was excavated and inventoried, since eggs are unlikely to hatch after this period (Dodd & Raybould 2014). During final nest inventories, the entire contents of the nest were removed, and all hatched and unhatched eggs were counted. Any live hatchlings found in the nest at the time of inventory were allowed to crawl to the ocean by themselves.

2.3. Nest environmental parameters

Two measures for nest temperature were calculated. First, we calculated the mean nest temperature throughout incubation, starting with the time the logger was placed into the nest and ending at 23:30 h on the day of hatching. The day of hatching was determined for all nests that successfully hatched by subtracting 4 d from the recorded emergence date, since it takes loggerhead hatchlings approximately that long to emerge from the nest after hatching (Godfrey & Mrosovsky 1997). For all nests where no hatching occurred, temperature records ended at 23:30 h on the day before inventory. Second, since there is a temperature range that is considered suitable for successful incubation (low of 26.5°C [Blair 2005], up to 34°C [Yntema & Mrosovsky 1982]), we calculated the number of hours above or below this acceptable range.

Nest moisture content was measured using an Aquaterr EC-350 digital soil moisture, temperature, and salinity meter (accuracy ±2 %), which measured moisture via capacitance, for each nest every 10 to 16 d (4–5 times per nest during incubation). Before each use, the probe end was submerged in water and calibrated to 100 % moisture. The probe was inserted into the sand ~15 cm to the right of the egg chamber when facing the dune so that measurements closely reflected the moisture content of the nest without puncturing any eggs with the meter, and readings were taken just below the sand surface as well as at depths of 20 and 40 cm below the surface. Moisture was averaged over these depths for a mean moisture content on each sample date. We acknowledge that surface moisture measurements may artificially depress estimates for nest moisture content, and so we consider these estimates to be conservative. Moisture readings were always taken between 06:00 and 09:00 h so that direct overhead sun had minimal effect on the amount of moisture present. The percent moisture of each nest was calculated by taking the mean value across all moisture recordings (i.e. approx. every 2 wk) for each nest during its incubation (Lolavar & Wyneken 2017).

A Trimble R8 real-time kinematic satellite navigation system was used to measure the elevation of nests above sea level in meters (accuracy ±0.02 m) within the North American Vertical Datum of 1988 (NAVD88) geodetic datum, US State Plane 1983 Georgia East Zone projection. Measurements were taken twice during the 2017 nesting season, once in June and once in August, to ensure that all nests were sampled and to reduce the chance of any major weather events destroying nests before data collection occurred. Measurements were taken once during mid-July for nests deposited in 2018. Due to equipment availability, elevation was measured for 164 nests. Vegetation was recorded after the initial nest excavation by placing a 1 m² gridded quadrat such that the nest was at the center of the quadrat.

Percent vegetation was calculated by counting how many of the 100 cells had any vegetation present. This method was repeated during the nest inventory to determine if vegetation cover changed during incubation.

The dip and strike of the dune face, or beach slope, of the nest were measured using a Brunton pocket transit using standard methods (Coe et al. 2010). The dip is the angle of the downward slope of the dune relative to the horizontal plane, which can range from 0 to 90°, as well as the direction of this slope relative to north. The strike is measured 90° from the dip and represents the planar dune face relative to north. These measurements indicate the direction the dune face slopes relative to strike (with a north reference) and the steepness of the slope of the dune face. Dip and strike measurements were taken 3 to 4 wk after the deposition of a nest. This allowed any sand disturbed by the nesting turtle to settle so a true shape of the dune could be measured.

2.4. Statistical analysis

The number of hatched eggs was calculated by counting the number of eggshells within the chamber that were at least 50% intact. The numbers of live and dead hatchlings found in the nest were also recorded. Hatch success (HS) was calculated using the following equation:

$$HS = (N \text{ hatched}/N \text{ total}) \times 100 \qquad (1)$$

where N hatched is the number of hatched eggs at the end of incubation, and N total is the total number of hatched and unhatched eggs at the end of incubation.

We developed a structural equation model (SEM) to estimate the direct and indirect effects of nest characteristics on HS (Grace et al. 2012). The SEM uses a hierarchical approach to estimate the overall effects of nest characteristics on hatching success by accounting for all potential pathways of effects. Based on the literature, we hypothesized that temperature, moisture, washovers, and clutch size would have direct effects on HS, whereas nest characteristics that are consequences of female nest site selection including elevation, vegetation cover, nest depth, lay date, strike, and dip would have indirect effects on HS (through effects on temperature, moisture, and washovers). Temperature variables included mean nest temperature, the number of temperature recordings >34°C (high temperatures), and the number of temperature recordings <26.5°C (low temperatures). We built the SEM in a Bayesian

framework using JAGS (Plummer 2003), run in the R version 3.5 environment (R Core Team 2020).

The observed number of hatchlings from each nest was binomially distributed so that for the ith nest:

$$h_i \sim \text{Bin}(p_i, N \text{ total}_i) \qquad (2)$$

where h_i is the number of hatchlings from nest i, p_i is the probability of hatching success, and $N \text{ total}_i$ is the total number of hatched and unhatched eggs at the end of incubation (Eq. 1). We modeled the direct effects of mean nest temperature, high temperatures, low temperatures, moisture, number of washovers, and clutch size on p_i as logit-linear effects. For the temperature variables, moisture, and number of washovers, we also modeled the indirect effects of nesting decisions. For mean nest temperature, high temperatures, and low temperatures, we estimated the linear effects of date, nest depth, elevation, vegetation percent cover, moisture, and strike and dip. For moisture, we estimated the linear effects of date, nest depth, elevation, vegetation percent cover, and strike and dip. For washovers, we estimated the linear effects of elevation, vegetation percent cover, and strike and dip.

All covariates were standardized using z-score scaling so that estimated effects could be directly compared for relative importance. For a given response variable, all predictor variables were uncorrelated ($|r| < 0.6$). We assigned uninformative uniform prior probability distributions to the hatching success response variable and uninformative normal priors to all other response variables (Table S1 in the Supplement at www.int-res.com/articles/suppl/m701p119_supp.pdf). We ran 3 independent Markov chain Monte Carlo (MCMC) simulations, discarding the first 10 000 MCMC samples as a burn-in and storing every fifth sample of the remaining 20 000 MCMC iterations for further analysis. We tested for Markov chain convergence to a stationary posterior distribution with the Gelman-Rubin diagnostic (Bolker 2008). We summarized posterior distributions for all parameters with the mean of all MCMC samples as a point estimate and the 2.5 and 97.5 percentiles of the MCMC samples as a 95% credible interval (Bolker 2008). To visualize the overall effect of nesting decisions on hatching success (while accounting for multiple indirect pathways), we calculated predictions of mean effects across the range of values sampled for influential nesting decision variables. We estimated the amount of variance explained by predictor variables for each response variable by computing pseudo R^2 values using linear regressions (Grace et al. 2012).

3. RESULTS

During the 2017 nesting season, the first nest was laid on 8 May and the final nest on 31 July, and 89 nests were initially sampled. The island had to be evacuated early due to Hurricane Irma, so the last nests of the season were sampled on 8 September. This resulted in 11 nests being lost from final inventory. An additional 9 of the sampled nests were lost to predation by either feral hogs *Sus scrofa* or raccoons *Procyon lotor*. In 2018, the first nest was laid on 15 May and the final nest on 3 August. A total of 111 nests were sampled during that season, although 9 were also lost to wild hog or raccoon predation. Therefore, 200 nests were initially sampled across both years, but due to losses from predation and Hurricane Irma, 170 nests were used for the subsequent analysis. Across all nests, hatching success ranged from 0 to 99.2%, with a mean of 46.2 ± 37.8% (mean ± SD). Of the 170 nests at the final inventory, no eggs hatched in 47 (27.6%).

The mean nest temperature for all nests was 29.7° ± 0.9°C. In nests which produced at least 1 hatchling, the lowest temperature recorded was 24.0°C, while the highest was 35.2°C. Approximately 36% of nests incubated completely within the optimal range of 26.5 to 32°C. Mean nest moisture, measured via capacitance, was 49.3 ± 18%, with a range from 5.4 to 89.6%. Seventy nests experienced at least 1 tidal washover across the 2 study seasons, while 1 nest (with 0% hatching success) experienced 24 tidal washover events during incubation (Fig. S1). With 2 exceptions, once the nest experienced >6 washover events, hatching success was zero. Dune vegetation was present around 54.7% of the nests (N = 93), with a range of 1.5% cover in the 1 m² area surrounding the nest to 87.5% cover when vegetation was present. Nest elevation ranged from 1.44 to 4.25 m above sea level, with a mean elevation of 2.09 ± 0.37 m, with similar elevations at all 4 beaches.

The SEM demonstrated that mean nest temperature and number of washovers were the most important predictors of hatching success (Fig. 2). While warmer nests that experienced fewer washovers had greater hatching success, the overall analysis indicated that nests that experienced both high and low temperatures as well as greater moisture all resulted in greater hatching success, while clutch size had a small negative effect on hatching success (Fig. 2). These effects explained a large amount of variance
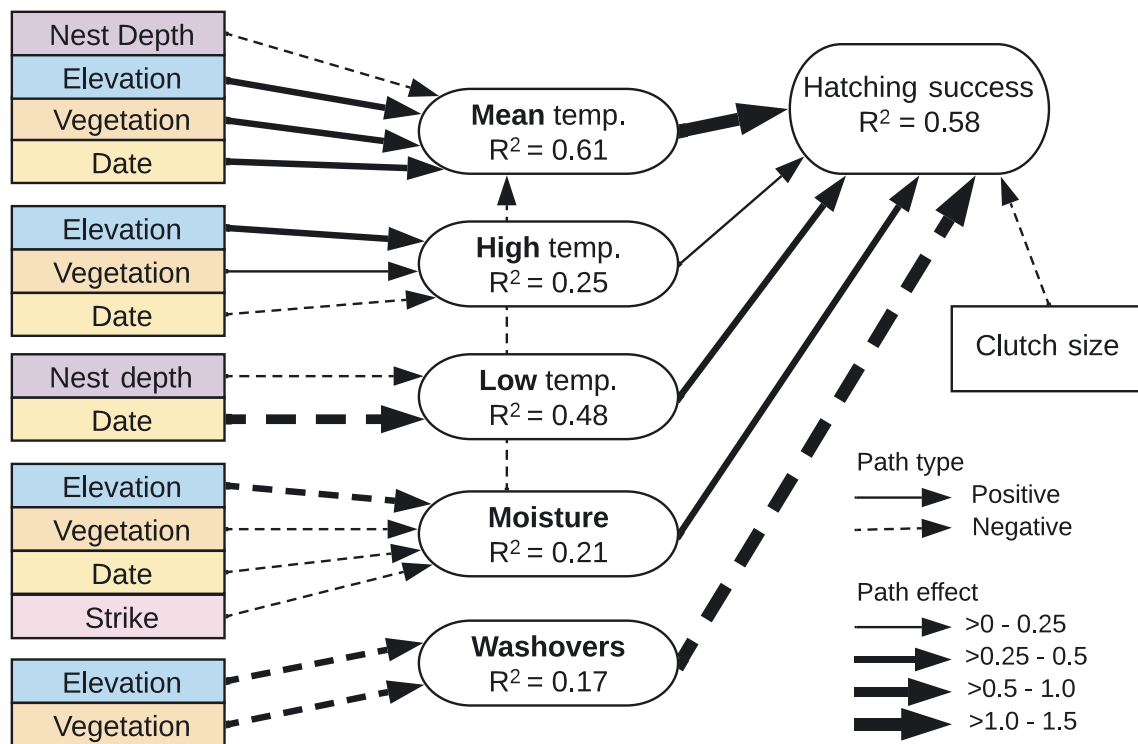

Fig. 2. Structural equation model of loggerhead sea turtle hatching success. Paths are only displayed for non-zero effects (i.e. 95% credible interval did not overlap with zero); additional paths were included in the model but are not displayed here. Arrow width indicates the absolute value of the median effect size for each standardized covariate
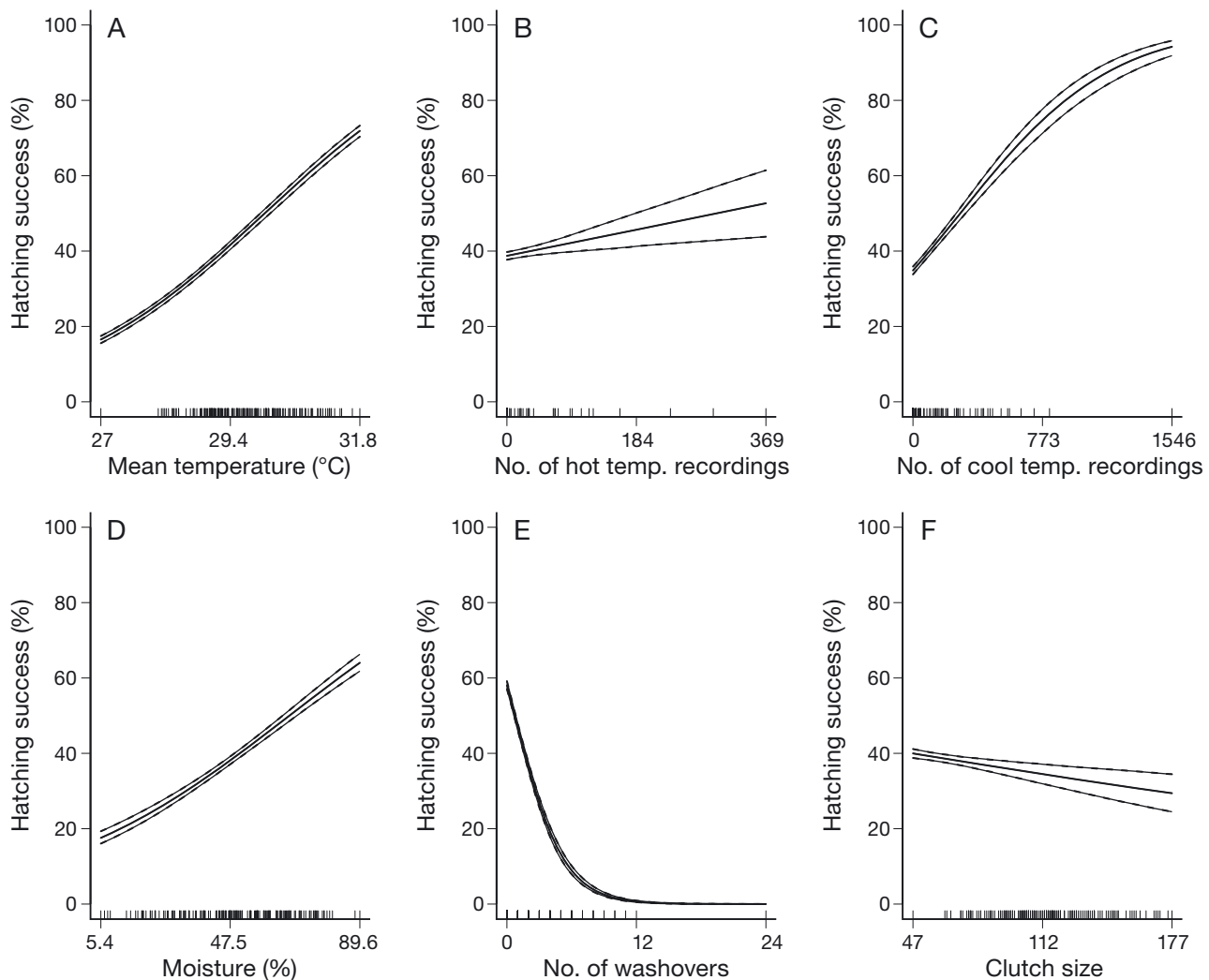
Fig. 3. Predicted effects of direct variables (A) mean temperature, (B) hot temperatures (>34°C), (C) cool temperatures (<26.5°C), (D) moisture, (E) washovers, and (F) clutch size, based on path estimates of a structural equation model of loggerhead sea turtle hatching success. Solid lines represent median predictions, and dashed lines represent 95% credible intervals. Predicted effects are from a multiple linear regression, so effects displayed are marginal effects after accounting for the effects of all other predictors, with non-focal effects held at their mean value. Tick marks on *x*-axes (data rugs) represent number of samples at each *x*-axis value

in overall hatching success ($R^2 = 0.58$). Mean nest temperature was highest in nests with later lay dates, greater vegetation cover, and higher elevations and lowest in nests with greater nest depth and greater moisture; these effects explained a large proportion of variance in mean nest temperature ($R^2 = 0.61$; Figs. 2 & 3A). High temperatures (>34°C; $R^2 = 0.25$; Fig. 3B) occurred more in high-elevation nests and those surrounded by vegetation, and fewer high temperatures occurred in nests that were laid later in the season. The high temperatures typically occurred later in the incubation period, likely reflecting seasonal temperature patterns, and occurred on diel cycles (Fig. 4, Figs. S2–S5). Low temperatures (<26.5°C; $R^2 = 0.48$; Fig. 3C) occurred less frequently in nests

with later lay dates and greater nest depths. When experienced, the lower temperatures occurred early in the incubation and exhibited diel cycles (Fig. 4, Figs. S2 & S6). Moisture ($R^2 = 0.21$; Fig. 3D) was lower in nests at higher elevations, with greater vegetation, later lay dates, and greater strikes (or more south facing). Washovers ($R^2 = 0.17$; Fig. 3E) occurred less frequently for higher-elevation nests and those surrounded by vegetation. Dip did not affect any of the intermediate response variables.

After accounting for all possible pathways of influence, elevation above mean sea level had the strongest effect of all the nesting decision variables on hatching success (Fig. 5B). Higher-elevation nests had greater hatching success, as these nests had both
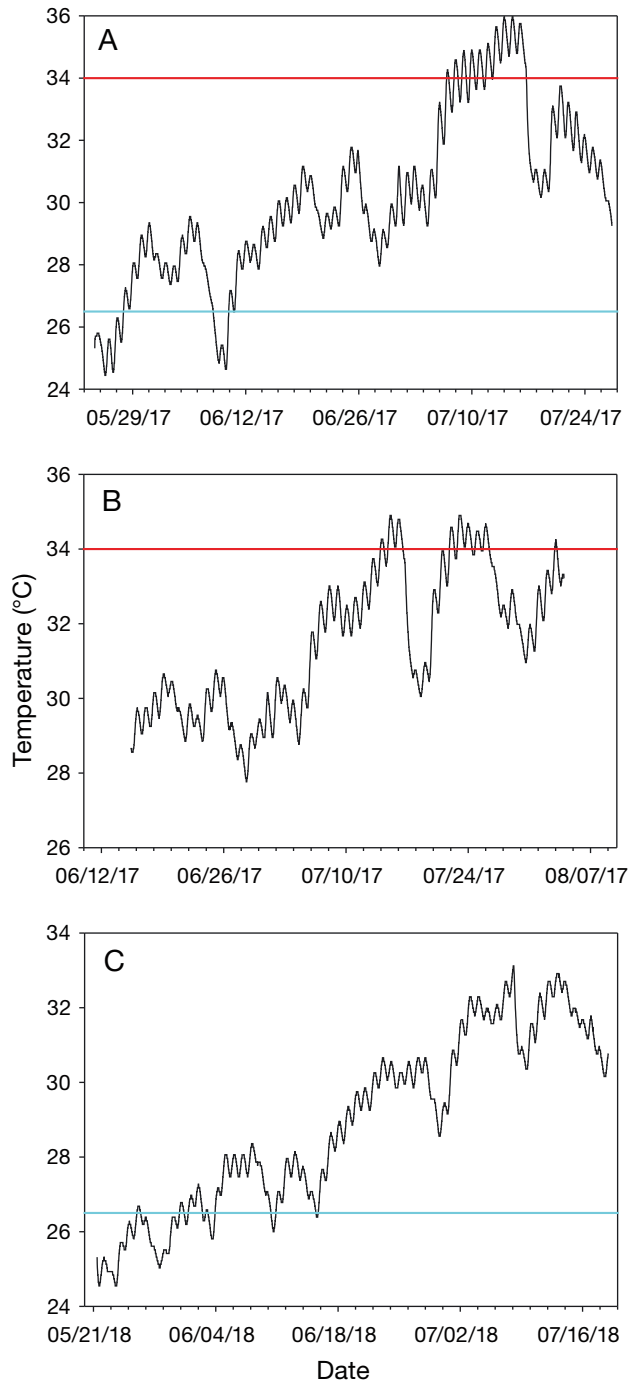
Fig. 4. Nest temperature profiles for (A) nest NB023, laid on 24 May 2017, which exhibited both extreme cold and extreme high nest temperatures and a 97% hatching success; (B) nest NM017, laid on 15 June 2017, which exhibited only extreme high nest temperatures and an 86% hatching success; and (C) nest NB004, laid on 21 May 2018, which experienced only extreme cold nest temperatures and an 86% hatching success. The red reference line is at 34°C, considered to be the upper threshold of suitable nest temperatures, whereas the blue reference line is 26.5°C, considered to be the lower threshold of suitable nest temperatures. Dates are presented as mo/d/yr

warmer mean temperatures and fewer washovers (Fig. 2). However, only a few very high elevation nests were sampled. Percent cover of vegetation also had a strong positive overall effect on hatching success (Fig. 5C). Hatching success was also slightly higher in nests with shallower chamber depths than deeper nests and in nests laid later in the nesting season (Fig. 5A).

4. DISCUSSION

Loggerhead sea turtle nest site selection decisions indirectly affect hatching success by impacting variables such as temperature, moisture, and tidal washover frequency, which can have strong direct effects. As expected, temperature (Mrosovsky 1988, Kobayashi et al. 2017) and washover frequency (Foley et al. 2006, Pike et al. 2015) had the strongest overall direct effects on loggerhead nest hatching success over the 2 yr of this study. However, by measuring a suite of variables *in situ* and using a hierarchical analytical approach, this study confirmed both important direct effects on hatching success as well as several indirect pathways (e.g. elevation, vegetation) that can influence these direct effects. Hatching success was affected by complex interactions of multiple nest site parameters, suggesting the importance of accounting for all the indirect pathways to understand how nest site location affects hatching success, providing valuable information for nest management strategies (i.e. relocation).

The observed positive relationship between temperature and hatching success was expected since temperature controls embryonic development (Bull & Vogt 1979, Bull 1980). The mean nest temperature in this study (29.7°C) was well within the accepted optimal range for loggerhead sea turtles (Yntema & Mrosovsky 1982, Blair 2005). However, 16% of nests experienced temperatures exceeding 34°C, the upper threshold of commonly accepted suitable nest temperatures, and even these high nest temperatures had an overall positive effect on hatching. Temperatures exceeding 34°C are thought to be lethal over long periods of time (Mrosovsky 1988), although nests can exceed temperatures of 34°C for short time periods and still exhibit high hatching success (Read et al. 2013, Howard et al. 2014). For the nests that did experience periods above 34°C, the period ranged from as little as 2 h of total logged time to over 1 wk of incubation period. Extreme high temperatures also tended to occur later in incubation, which could demonstrate a seasonal effect or could be related to metabolic heat
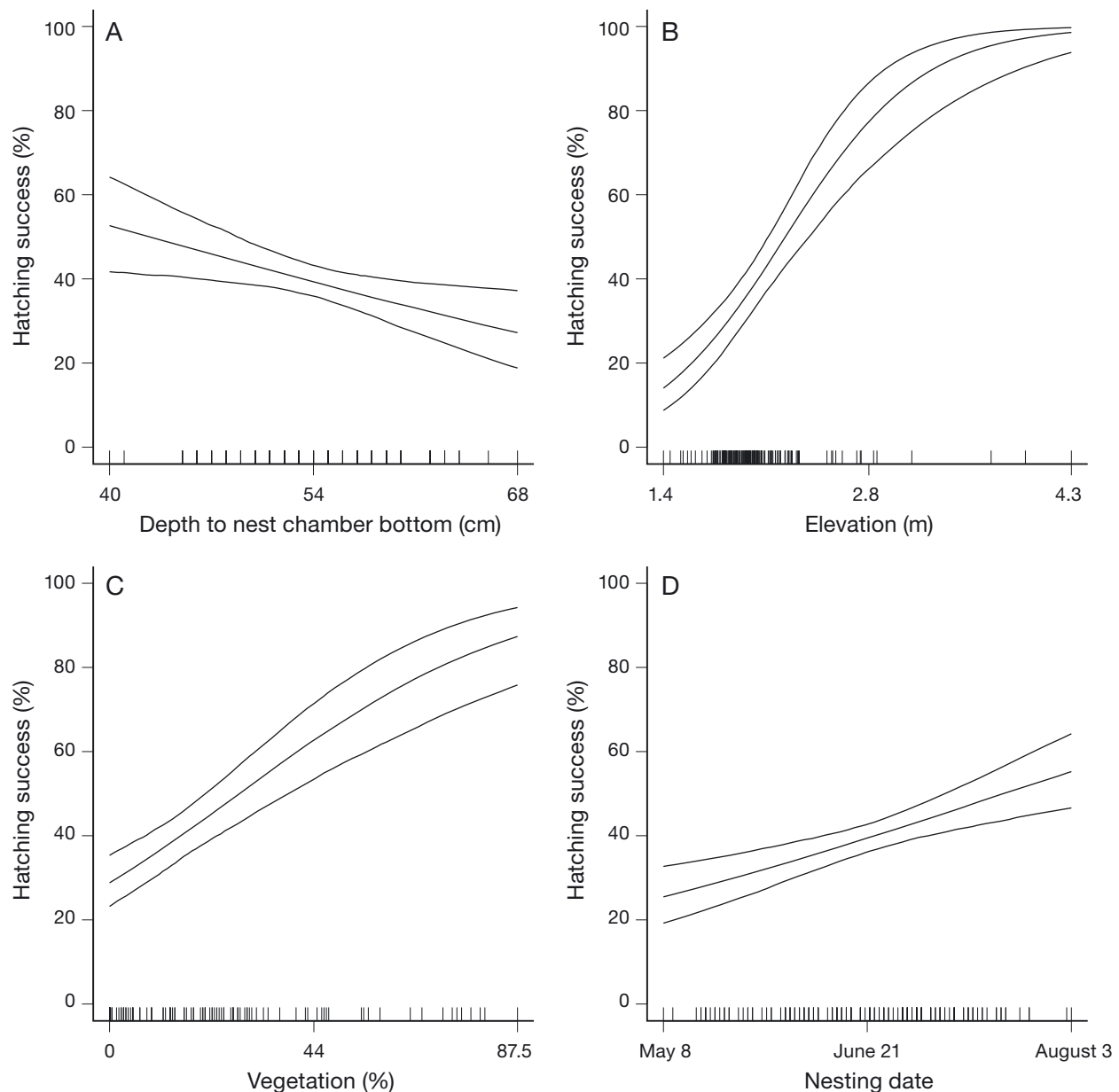
Fig. 5. Predicted effects of nesting decisions (A) chamber depth, (B) elevation, (C) vegetation, and (D) nesting date, based on path estimates of a structural equation model (SEM) of loggerhead sea turtle hatching success. Solid lines represent median predictions, and dashed lines represent 95% credible intervals. Predicted effects are from multiple linear regressions, so effects displayed are marginal effects after accounting for the effects of all other predictors, with non-focal effects held at their mean value. Predictions account for all pathways connecting the nesting decision variable to hatching success within the SEM (i.e. after accounting for effects of direct variables in Fig. 3). For instance, nesting date has a negative effect on moisture and the number of temperature readings below a cold threshold (low temperature), which would result in a negative effect of date on hatching success, but since nesting date also has a positive effect on mean nest temperatures, the overall effect of nesting date on hatching success is positive. Tick marks on *x*-axes (data rugs) represent number of samples at each *x*-axis value

from the developing embryos (Gammon et al. 2020). Additional study of when temperature extremes occur within the incubation period may help elucidate the mechanism driving hatching success.

Frequency of tidal washovers also had a strong negative effect on hatching success in this study, con-

sistent with other sea turtle studies (Wood & Bjorndal 2000, Foley et al. 2006). While most nests can withstand minimal and brief tidal inundations without drastic impacts on hatch success if they occur outside critical early and late incubation periods (Limpus et al. 2020), nests more frequently inundated by tides

experience low hatch success (Foley et al. 2006). Thus, timing (Limpus et al. 2020), frequency (Pike & Stiner 2007), and length (Pike et al. 2015) all influence the impact of tidal inundations on hatching. In this study, hatching success decreased with increasing frequency of washovers, and with 1 exception, when a nest reached 6 washovers during the nesting period, no hatchlings emerged. However, washover frequency may be mitigated by other nest variables that affect nest drainage (Foley et al. 2006), and inundations occurring outside critical incubation periods may have minimal negative impacts (Limpus et al. 2020). Understanding how timing, frequency, and length of inundations affect hatching success may be critical to develop appropriate management strategies for projected sea level rise (Pike et al. 2015).

Inundations may affect hatching success through increased nest moisture, where high moisture may delay development and increase mortality by impeding gas exchange between eggs and the environment (Marco et al. 2017), lead to embryo asphyxiation (Wood & Bjorndal 2000, Foley et al. 2006), and decrease hatching success (Özdemir & Türkozan 2006). However, by accounting for all other nest variables, we found that nest moisture content had an overall positive effect on hatching success, as other studies have found (Bustard & Greenham 1968, Lolavar & Wyneken 2021). Any direct effects of moisture per se may also be confounded by other variables, such as temperature (Godfrey et al. 1996, Lolavar & Wyneken 2015). Moisture reduces mean nest temperature, which can prolong incubation (McGehee 1990) and alter sex ratios (Lolavar & Wyneken 2017). The combination of direct and indirect pathways may explain the array of effects observed in other studies, demonstrating the utility of an analytical framework that can parse out both types of pathways.

After accounting for all potential pathways for all measured variables, elevation had the strongest positive effect on hatching success. Higher elevations reduce the incidence of tidal inundation (Foley et al. 2006) and, in this study, experienced higher nest temperatures. Higher-elevation nests will become increasingly important as tidal inundation increases with sea level rise (Pike et al. 2015), which could affect successful nests and optimal nesting location (Hawkes et al. 2007, Brantley et al. 2014). Although there was a positive relationship in our study, most of our nests were found in a relatively narrow 1 m band of elevation. Very high elevations could reduce overall hatching (Horrocks & Scott 1991) because they are likely to be drier (Whitesell 2018), are at elevated risk of predation (Blamires et al. 2003), and may skew sex ratios (Foley et al. 2000, Patrício et al. 2017), so we caution against overinterpretation at elevations above 2.5 m NAVD88, which were rare in our dataset.

Vegetation cover around the nest chamber also had a strong positive effect on hatching success when accounting for all the different pathways. The presence of vegetation may affect the microclimate of the nest (Staines et al. 2019), resulting in altered nest temperatures and moisture content (Bustard & Greenham 1968, Ferreira Júnior et al. 2008). Large vegetation which casts shade can affect both hatching success and resulting sex ratios (Patrício et al. 2017). Nesting in vegetation can lead to high hatching success (Garmestani et al. 2000, Cabrera Guerra et al. 2021). Alternatively, nesting attempts may fail (Hays & Speakman 1993) or be limited within vegetation (Serafini et al. 2009), and nests can exhibit relatively reduced hatching success (Conrad et al. 2011, Staines et al. 2019). The variable nature of the literature suggests potential plant species- and site-specific effects of vegetation on sea turtle hatching. In our study area, the plants were primarily narrow-leaved grasses and sedges with soft rhizomes that were unlikely to impact digging or shade nests.

Critically, the hatching success outcomes derived from relationships with measured variables may be confounded by the effects of each variable on sex determination. While warmer nests lead to higher overall hatching success, warmer nests also skew sex ratios and produce more female offspring (Bull & Vogt 1979, Georges et al. 1994, Jensen et al. 2018). Several of the measured variables in this study, such as elevation, moisture, chamber depth, and vegetation, may also indirectly influence sex ratios by modulating the nest temperature environment (Lolavar & Wyneken 2017, Marco et al. 2018, Patrício et al. 2017). Warmer nests that more successfully produce predominantly female offspring may have negative consequences for overall reproductive success, although little is known about operational sex ratios of breeding adults, which may be as high as 1 male to 7.5 females (Schofield et al. 2017). Using equations for estimating sex ratios in Georgia (LeBlanc et al. 2012), Whitesell (2018) predicted that although there was an overall female-biased sex ratio across both study years, some nests were likely to produce up to 60% (2018) to 83% (2017) males. Therefore, exploring how the complex set of variables that affect hatching success on nesting beaches may also interact to affect sex ratios of the hatchlings could be considered in the future.

This study indicates that climate change is likely having complex effects on sea turtle populations. Within the context of hatching success, a warming

climate might initially benefit loggerhead turtles, particularly populations that nest near the leading edge (or cooler climate) of the species' geographic range (Montero et al. 2019). The northern range limit for loggerhead turtles is at least partially determined by temperature — beaches substantially further to the north may not have sufficiently warm or long summers to successfully incubate eggs. Therefore, a warming climate may make nest incubation conditions more conducive for higher hatching success, potentially leading to larger annual cohorts. Improved reproductive success at the leading edge of geographic ranges with increasing temperatures have been demonstrated for plants (Dangremond & Feller 2016, Ordoñez-Salanueva et al. 2021) and invertebrates (Ling et al. 2008) and recently observed in gopher tortoises *Gopherus polyphemus* (Hunter et al. 2021). However, warming temperatures could influence hatchling sex ratios, skewing toward a female bias (Hawkes et al. 2007, Reneker & Kamel 2016, Jensen et al. 2018), although turtles may compensate by choosing different elevations or digging deeper nests (Hays et al. 2001), and temperatures could also be modulated by changes in precipitation and nest moisture (Lolavar & Wyneken 2015). Longer term, rising seas associated with warming climates could alter and reduce available nesting habitat (Brantley et al. 2014) and potentially affect the frequency of tidal washovers at high tides (Pike et al. 2015).

Our results also have several management implications for endangered sea turtle populations. Many efforts conduct nest relocation to higher elevations to help boost hatching success, and our study supports this practice. Particularly, moving nests out of low-elevation areas where they are too cool and have a high probability of being washed over to higher-elevation areas with vegetation is likely to improve hatching success. Our model explained >60% of the variance in mean nest temperature, suggesting that using critical information (i.e. elevation, vegetation) to select relocation sites, and digging an appropriate chamber depth, can significantly enhance hatching success. Further, moisture also had a positive influence on hatching but tends to be lower in the areas where temperature is higher, suggesting that mechanisms to boost moisture on relocated nests (i.e. watering; Lolavar & Wyneken 2021) may further enhance hatching success in managed populations. Watering (LeBlanc & Wibbels 2009, Smith et al. 2021) and shading (Esteban et al. 2018, Vindas-Picado et al. 2020) high-elevation nests as a means of reducing temperatures could also improve resulting hatchling sex ratios. We caution relocating to very high elevations (i.e. 3–4 m) without further study, since high elevations could limit hatching success (Horrocks & Scott 1991) and were poorly represented in our study. Regardless of elevation, vegetation at sandy beaches, particularly grasses and sedges, could also be used to identify relocation areas for improved hatching success (Serafini et al. 2009).

In conclusion, by sampling multiple variables that could affect hatching success on nesting beaches, we were able to explain a high amount of variance in hatching success through both direct and indirect pathways. Temperature was the most important factor influencing successful hatching, where increasing temperatures, even temperatures above 34°C, led to higher hatching success. This has important near-term implications as sea turtle species face changing climates. Long-term changes in sea level due to climate will likely decrease hatching success by increasing washover frequency unless turtles can alter their beach nesting behavior and/or more direct management is applied. Further, this study highlights how beach variables influence the incubation environment within the nests and provide critical information to build predictions about how environmental changes or different management practices might influence hatching success and subsequent population increases in sea turtles. This research underscores the importance of collecting multiple parameters and using hierarchical analytical approaches for the management of threatened and endangered species. Future research can use these approaches to map critical nesting areas for present management practices as well as predict critical nesting areas in future warming, sea level rise, and even nesting habitat loss scenarios.

Georgia DNR Scientific Collecting Special Purpose Permit No. 27067 and approved by Georgia Southern IACUC No. I17009.

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