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Environmental Factors Affecting Hatch Success in the Loggerhead Sea Turtle (Caretta caretta)

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ENVIRONMENTAL FACTORS AFFECTING HATCH SUCCESS IN THE LOGGERHEAD SEA TURTLE (*CARETTA CARETTA*)

by

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(Under the Direction of John M. Carroll)

ABSTRACT

The loggerhead turtle (*Caretta caretta*) is a species federally listed as "threatened" whose global populations are declining. Georgia Department of Natural Resources conservation protocols for this species require the daily monitoring of nesting activity and permit physical relocation of nests which are at risk of being eroded or flooded by storms and high tides in order to increase hatch success--the proportion of hatched to unhatched eggs. Relocated nests are moved to an area with higher elevation in order to avoid flooding, but other variables such as increased temperature and decreased moisture are introduced when relocating. For years temperature and moisture have been regarded as the most important factors that contribute to hatch success but these variables are not always directly considered when relocating nests. It is likely that other environmental variables have an effect on hatch success and influence temperature and moisture.

The hypothesis that a combination of geological and biological factors better predicts hatch success compared to temperature and/or moisture alone was tested. Secondly the environmental variables which influence temperature, moisture, and likelihood of tidal washover were also examined to evaluate their impact on hatch success. Loggerhead nests on Ossabaw Island, Georgia were monitored throughout incubation; upon incubation completion, hatch success was calculated. For all nests, temperature, moisture, vegetation cover and composition, elevation, dune morphology, and tidal washovers were recorded. These variables were analyzed to assess their individual and combined influences on nest conditions and ultimately on hatch success. In addition to number of washover events, temperature, and moisture, nest vegetation and elevation were important predictors of hatch success in loggerhead sea turtle nests and should be considered when nest relocation is required.

INDEX WORDS: *Caretta caretta*, Loggerhead sea turtle, Hatch success, Sea turtle conservation, *Chelonia*, Beach morphology, Wildlife management

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by

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DEDICATION

This document is dedicated to Mrs. Cathy Chamberlin Graham whom without I would not have been as successful as an undergraduate student nor decided to pursue graduate school. She encouraged me to follow my dreams when I thought they were out of reach and always challenged me to do my best. Along with her husband and my undergraduate advisor, John Graham, I was always academically and emotionally supported. Thank you for emboldening me to follow this dream of a project.

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CHAPTER 1

INTRODUCTION

There are seven species of sea turtles extant in our world today. Globally-recognize d species include the leatherback (*Dermochelys coriacea*), flatback (*Natator depressus*), Kemp's ridley (*Lepidochelys kempii*), olive ridley (*Lepidochelys olivacea*), green turtle (*Chelonia mydas*), hawksbill turtle (*Eretmochelys imbricata*), and the loggerhead turtle (*Caretta caretta*), although there is some debate that more species exist (Spotila 2004). All sea turtle species are classified as Vulnerable, Endangered, or Critically Endangered as defined by the International Union for the conservation of Nature (IUCN) Red List with globally decreasing population trends (except for *N. depressus* which is defined as Data Deficient). The loggerhead sea turtle is the most common sea turtle nesting on the Atlantic coast of the United States and is the most studied sea turtle in the world (Spotila 2004). *Caretta caretta* is a globally Vulnerable and Endangered species as defined and identified by the IUCN Red List, however increasing nesting trends over the past two decades indicates that the Northwest Atlantic subpopulation is increasing (Casale and Tucker 2017). The majority of loggerheads in the United States nest on beaches ranging from Florida to North Carolina including all Georgia barrier island beaches, as well as parts of Alabama and Texas (Ehrhart et al. 2003; NMFS and USFWS 2008; Witherington and Witherington 2011).

In the eastern United States, loggerheads are major consumers of horseshoe crabs (*Limulus polyphemus*), hermit crabs (*Pagurus pollicaris*), echinoderms, spider crabs (*Libinia* spp.), whelks (*Busycon* spp.), other invertebrates, and fish bycatch from trawlers, (Ruckdeschel and Shoop 1988; Youngkin 2001). Loggerheads are also important prey items in marine systems, particularly for apex predators (*eg.* great white and tiger sharks; Fergusson et al. 2000; Heithaus et al. 2002). Loggerhead sea turtles provide novel habitat to many epibiont species which reside on the carapaces and plastrons of most adult sea turtles (Bjorndal 2003; Witherington and Witherington 2015). Loggerheads appear to host the most diverse range of epibionts of all sea turtle species (Bjorndal 2003), and multiple studies have described over 100 epibiont species living on loggerheads nesting in Georgia (Frick et al. 1998, 2000).

Beyond ecological importance, *Caretta caretta*, among other sea turtle species, have become popular, charismatic megafauna that grasp the interest of tourists and citizen scientists (reviewed in Cazabon-Mannette et al. 2017). Many beaches where sea turtles nest host events where people can volunteer to monitor beaches. This increased interest in an endangered megafauna species that relies on both terrestrial and marine habitats to complete its life cycle can be a major tool in conservation management because people are willing to pay to encounter sea turtles in the wild and to preserve their habitats making loggerheads a keystone species whereby their protection yields protection for other species (Whitehead 1992; Cazabon-Mannette et al. 2017). Because of its widespread presence on the East Coast, *Caretta caretta* can be an ambassador for endangered or threatened marine wildlife and beach conservation. Federal protection under the Endangered Species Act and critical habitat designation for several Georgia nesting habitats are afforded for this species (NMFS and USFWS 2008). For these reasons, there are considerable efforts to restore historical populations and maintain habitat for this species. For example, all sea turtle nests in Georgia are identified and monitored for the duration of nest incubation.

While monitoring and protecting nests are important, most conservation plans also call for nest relocation. For example, nests laid close to the spring high tideline are more likely to be inundated by tides which can decrease hatch success (Foley et al. 2006). Current conservation plans suggest that nests laid at sites below the spring high tide line be relocated to areas of higher elevation to increase nest hatch success, or the proportion of hatched to unhatched eggs in each nest (NMFS and USFWS 2008). This drastic step is taken since hatch success is vital for the recovery of endangered and threatened marine turtle populations (Dutton et al. 2005). The egg is arguably the most vulnerable stage of life for loggerheads (Özdemir et al. 2008; Sim et al. 2015) with previous studies reporting up to 21% egg mortality within the nest (see Özdemir et al. 2008). The majority of overall mortality in loggerhead populations occurs within the first year of life (Ascani et al. 2016) with an estimated 10-30% of eggs laid surviving to become year old hatchlings (Frazer 1986). Since the incubation period is critical, nest relocation is an important tool used by management agencies to increase hatch success (Dutton et al. 2005; Tuttle and Rostal 2010; Ilgaz et al. 2011) while still allowing nests to incubate on nesting beaches as opposed to incubating in hatcheries.

A number of environmental factors influence hatching success, and it is important to consider environmental variables when choosing sites for nest relocation. In particular, temperature is considered among the most important environmental parameters which affect hatch success (Bull 1980; Wibbels 2003; Blair 2005). For example, the suitable temperature range for incubating loggerhead nests is 26.5 - 32°C (Bull 1980; Wibbels 2003; Blair 2005), and maybe up to 34°C (Yntema and Mrosovsky 1982), and incubation temperatures outside of this range may lead to lower hatch success or doom the nest entirely (Blair 2005; Bull 1980; Wibbels 2003; Yntema and Mrosovsky 1982). These temperature ranges are particularly concerning since climate change is likely to make many nests within the current loggerhead nesting range exceed the suitable range within years or decades (Butt et al. 2016). Many studies have examined the effects of temperature on nests incubating under lab conditions (Bull and Vogt 1979; Bull 1985;

Georges et al. 1994; Howard et al. 2014), so it is important to also assess nest temperature in relation to successful incubation conditions *in situ*.

A second major factor that can influence loggerhead hatch success is nest substrate moisture (Wood and Bjorndal 2000; Lolavar and Wyneken 2015; Wyneken and Lolavar 2015). For example, nests at low elevations experience higher moisture as a result of more frequent tidal inundation and experience lower hatching success (Foley et al. 2006), making inundations a major concern for monitoring, relocation, and conservation efforts. Too much or too little moisture in a nest can result in decreased hatch success (Carthy et al. 2003), although there is some debate about ideal nest moisture. McGehee (1990) found 25% moisture to be ideal for successful incubation with decreased hatch success at lower and higher moisture levels. High nest moisture during incubation can impede gas exchange between the egg and the environment, delaying development and increasing mortality, while also impeding the ability of hatchlings to emerge successfully (Marco et al. 2017). However, the effects of nest moisture on hatch success are unclear, with some studies demonstrating moisture effects (Lolavar and Wyneken 2015), and others showing no impact of moisture (Foley et al. 2006; Horrocks and Scott 1991; Wood and Bjorndal 2002), and effects may be confounded by moisture's relationship to nest temperature (Godfrey et al. 1996; Yntema and Mrosovsky 1980).

Tidal washover and nest inundation are important factors which lead to decreased hatch success in sea turtle nests (Wood and Bjorndal 2000; Foley et al. 2006; Brig 2014). Nests that are washed over and inundated by tides usually experience high rates of embryo mortality thereby decreasing hatch success (Wood and Bjorndal 2000) as a result of embryo asphyxiation (Foley et al. 2006). However nests that are only partially washed over or that only experience inundations once or twice may still produce viable hatchlings (Foley et al. 2006). Freshwater inundations of nests may also occur after heavy rain events. Georgia barrier island beaches have relict marsh mud beneath the sand which may result in heavy precipitation draining slowly once it passes through the thin sand layer above the mud (Bishop et al. 2011). Nests laid at lower elevations are closer to this mud and are more likely to be inundated by a perched water table (Bishop et al. 2011). Tidal washover and inundation may dramatically affect hatch success depending on the frequency and intensity of washover events.

While temperature, moisture, and tidal washover are considered important drivers of hatch success, a number of other variables on nesting beaches can influence either or both of these drivers. For example, vegetation can be an important driver of both temperature and moisture content. Potential effects, depending on plant species and density, include shading to reduce temperature and moisture loss, minimizing heat transfer, or a drying effect from transpiration (Fowler 1979; Ferreira Júnior et al. 2008). There has been relatively little research correlating vegetation and hatch success in turtles. For green turtles (*Chelonia mydas*), nests at or within the vegetation line have decreased incubation periods compared to nests laid at low- or mid-beach locations (Fowler 1979). Nests of the hawksbill turtle (*Eretmochelys imbricata*) had higher hatch success when laid on open beach compared to nests laid more than 1 m into vegetation (Ditmer and Stapleton 2012). A study analyzing vegetation and the freshwater painted turtle (*Chrysemys picta*) indicated that decreased vegetation led to increased hatch success (Warner et al. 2010). No studies have analyzed vegetation in relation to hatch success in loggerhead turtle nests, although Ferreira Júnior et al. (2008) suggest that vegetation may be a factor to consider when choosing locations for nest relocation. For example, vegetation could be harmful to nests due to nest invasion by root systems (Witherington 1986). Vegetation may play an important role in nest site selection in some beach habitats utilized by *C. mydas, C. caretta, E.*

imbricata, and *D. coriacea* as the nesting turtles cue into the presence of vegetation as an indicator of nesting habitat (Fish et al. 2005; Fujisaki et al. 2018). Vegetation may be an important indicator of good nesting habitat especially as beach habitat is expected to change in the face of a changing climate (Fish et al. 2005; Fujisaki et al. 2018). It remains unclear how beach dune vegetation influences either temperature or moisture and ultimately hatch success of loggerhead nests.

In addition to vegetation, elevation of the nest above sea level can also influence a number of other nest environmental conditions. This is especially important since elevation is usually the metric used when determining nest relocations. For example, nests in higher elevations result in higher incubation temperatures and increased hatch success (see Pfaller et al. 2009; McNeill et al. 2016). However, other studies demonstrate that nests relocated to areas of higher elevations may result in decreased hatch success due to high average temperatures and decreased moisture (Lolavar and Wyneken 2015; Tomillo et al. 2014; Hays et al. 2017; Kobayashi et al. 2017). Horrocks and Scott (1991) found that *E. imbricata* nests laid above or below an average elevation for their study site (1.11m) experienced decreased hatch success suggesting that some turtles may select nest sites based on elevation. Further, they suggest that hatch success is generally positively correlated with elevation (Horrocks and Scott 1991). Although elevation may serve as a major cue for nesting in loggerheads (Wood and Bjorndal 2000), the relationship between elevation and hatch success is still unclear and requires further attention.

Finally, dune morphology may play a role in nest site selection by turtles (Wood and Bjorndal 2000), while also affecting the other environmental parameters. Specific dune morphology might affect nest environments as the sun strikes nest sites at different angles, intensities, and for varying time per day (R. Kelly Vance, *personal communication*). Nests in locations where the strike of the dune results in more direct morning or mid-day sun could have warmer incubation temperatures and decreased moisture compared to nests on dunes with strikes that result in less direct morning sun and more late-day sun, which tends to be less intense in comparison (Lavallin 2015). The dip of the sea side (generally the windward side) of a dune could also impact incubation conditions. A nest on a dune that has a steeper dip (the slope relative to a horizontal plane) may have more direct early morning sunlight resulting in accelerated early morning heating, and it may have better drainage leading to decreased moisture compared to a nest with lower dip angles.

It is currently unclear which environmental factor or combination of factors have the greatest impact on loggerhead hatch success, and this information is critical for nest management and relocation strategies to be successful. Further, the factors that currently limit hatch success are likely to be exacerbated under future climate conditions. For example, warming air temperatures will likely result in warming nest temperatures. Precipitation volume and patterns are expected to change in coming years which will alter nest moisture, sand temperatures, and vegetation composition on dunes (Feagin et al. 2010). As sea level changes, most Georgia barrier islands are experiencing erosional loss of dunes (Griffin and Henry 1984, Meyer 2013; Bishop et al., *unpublished data*). By better understanding how these factors affect hatch success, we can update management protocols to increase efficiency in conservation efforts by concentrating relocation efforts only on high-risk nests, selecting optimum sites when relocation is necessary, and be better prepared to deal with climate change-related obstacles in the future. Specifically, in coastal Georgia, the relocation efforts require many man hours and resources (Mark Dodd, GA Department of Natural Resources Sea Turtle Program Coordinator, *personal* *communication*). Therefore, my main objective was to explore how a collection of environmental parameters–temperature, moisture, vegetation, elevation, distance from the tideline, dune morphology, and tidal inundation–may interact to affect hatch success in loggerhead sea turtle nests on a Georgia barrier island. Specifically, I tested the following hypotheses: 1) Nest site biotic and abiotic variables will affect nest temperature, moisture, and likelihood of nest washover; 2) Vegetation within the immediate vicinity of the nest has an indirect effect hatch success; 3) Nests deposited at higher elevations and nests on dunes with steeper dips will be associated with higher temperatures, lower nest moisture and lower likelihood of tidal washover. Combined, this information can be vital for sea turtle nest management both within Georgia and throughout the loggerhead range.

CHAPTER 2

METHODS

Study Site

Sea turtle nest monitoring was conducted on Ossabaw Island, Georgia's third largest barrier island (31.77°N -081.08°W; Figure 1; Appendices 1-8). The climate on Ossabaw is categorized as humid subtropical with generally hot summers and mild winters (Peel et al. 2007). Ossabaw Island is managed by the Georgia Department of Natural Resources, and is only accessible by boat with very limited public access. The island's oceanside coast consists of five non-consecutive beaches which total 17.1 km for potential sea turtle nesting habitat. Ossabaw Island is undeveloped and has light human influence, as such, no man-made structures such as sea walls obstruct sea turtles' access to these beaches. Further, due to limited accessibility, there is little direct human impact to turtle nests.

Initial Nest Excavation and Monitoring

All beaches on Ossabaw Island were monitored daily during Georgia's nesting season (May 5 - September 8, 2017; May 3 - September 26, 2018) beginning at first daylight approximately 30 minutes before sunrise. Sampling was shortened in 2017 due to Hurricane Irma. Every morning, I identified new nests by locating crawlways which indicated a female turtle attempted to nest the previous night. At the apex of the crawlway, a number of indicators were used to determine whether a nest was laid–ripped vegetation, thrown sand, and the presence of a body pit (Figure 2). When one or more of these signs were present, I probed the body pit with a 1m long stick to locate the egg chamber. This method was used because the surface sand above the egg chamber will be less compacted compared to surrounding areas which were not disturbed by the turtle (Brig 2014). When the probing stick sank through soft sand, the sand was removed by hand until the top of the egg chamber was located. Upon finding eggs, the nest was assigned a reference number and GPS coordinates were taken.

Nests in this study were selected in an attempt to keep the sample proportional to the population of nests on each of the five beaches (*ie*. if 50% of island nests were located on North Beach, approximately 50% of the selected sample were North Beach nests). The frequency which nests were added to the sample was likewise proportional to the number of nests up to that point in time based on the number of new nests deposited daily. Based on Ossabaw nesting history from 2012 - 2016 nesting seasons (GADNR, *unpublished data*), 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. However because of the unpredictable nature of female site selection, it was impossible to select nests at complete random.

From all nests selected for sampling, I removed and counted all eggs and placed them into a bucket with cool, moist sand. I measured the total depth of the nest and then began to return the eggs. After counting eggs, I returned half of the clutch to the nest chamber first, and then placed a HOBO Pendant® Temperature Data Logger (accuracy ± 0.53°C) set to record temperature at 30 minute intervals attached to nylon mason line into the nest. The logger was placed in the middle of the nest approximately halfway from all sides of the nest chamber. I then placed the remaining half of the eggs back into the nest. The eggs were re-covered with sand in order to recreate how the mother tamped down sand over the eggs during oviposition. Egg removal occurred between the hours of 06:20 and 10:30 (with the exception of 9 nests which were discovered when beach monitoring lasted into the afternoon). In total, eggs were kept out of the chamber for no more than 10 minutes before being replaced. When eggs are removed within

12 hours of oviposition, it is generally considered to do little harm because the embryo has not yet attached to the wall of the egg (Mrosovsky 1988).

Three metrics were used for nest temperatures. I calculated the mean nest temperature throughout incubation, starting with the time the logger was placed into the nest and ending at 23:30 on the day of hatching. The day of hatching was determined for all nests that successfully hatched by subtracting four days from the recorded emergence date since it takes loggerhead hatchlings approximately that long to emerge from the nest after hatching (Godfrey and Mrosovsky 1997). For all nests where no hatching occurred, temperature records ended at 23:30 on the day before inventory. Second, since there is a temperature range that is considered suitable for successful incubation (26.5 - 32°C as defined by Blair 2005; Bull 1980; Wibbels 2003), I calculated the number of hours outside this acceptable range. However, since some literature suggests that some clutches may be able to withstand incubation up to 34°C (Yntema and Mrosovsky 1982), I also calculated the number of hours above this extreme temperature. Finally, for all nests which produced one or more hatchlings, the average temperature during the middle third of incubation was calculated to estimate hatchling sex ratios based on methods in LeBlanc et al. (2012).

After counting eggs, I recorded vegetation around the nest by placing a 100 cell, 1 m^2 quadrat grid over the nest so that the center of the nest was in the center of the quadrat. Percent vegetation was calculated by counting how many cells had any vegetation present in them. This method was repeated during the nest inventory to determine if vegetation cover changed during the course of incubation. If vegetation was present around the nest at the time of nest inventory, a photo was taken so plants could be identified. All plants were identified to general taxonomic group according to Witherington and Witherington (2011) and placed into one of three categories: grasses, sedges, or herbs and flowers.

Nests were then covered with a plastic screen approximately 1.2 m x 1.2 m and staked down at the four corners with metal pencil rod to deter potential predators. Each nest was identified by a 1m long wooden stake hammered into the ground approximately 0.5 m shoreward of the egg chamber. At this time, a line was drawn on the stake indicating the sand height. This line was used as the reference for nest height when measuring nest elevation later in the season. I then measured the distance from the surface of the sand above the egg chamber to the previous night's high tideline (DTL).

The dip and strike of the dune face, or beach slope, hosting the nest were measured using a Brunton pocket transit according to methods in Coe et al. (2010). The strike of a planar geological feature is line produced by the intersection of the planar feature with a horizontal plane. The compass orientation of this line may be recorded as an azimuth. In this case, the planar geological features are the dune faces where nests are laid. Strike azimuths range from 0 - 359° (where 360°=0° or due north). The dip is the inclination or slope of that planar geological feature relative to a horizontal plane. The dip is measured 90° from the recorded strike. Dip includes two measurements–dip magnitude and dip direction (Figure 3). The dip magnitude refers to the degree of slope of the feature relative to the horizontal plane. Dip ranges from 0 to 90 degrees. A flat surface is 0 degrees. Because the strike could dip one of two ways (180° difference) a dip direction is given to define direction of the slope. These measurements indicate the direction the dune face slopes relative to strike (with a north reference), and how steep the slope of the dune face is. Dip and strike measurements were taken 3-4 weeks after the deposition of a nest. This was done to allow any sand disturbed by the nesting turtle to settle so a true shape of the dune could be measured.

A Trimble R8 real-time kinematic (RTK) satellite navigation system was used to measure the elevation of nests above sea level in meters (accuracy ± 0.02 m) within the 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. For elevation, I used point data for each nest. Due to equipment availability, elevation was measured for 164 nests.

I measured nest moisture content using an Aquaterr EC-350 Digital Soil Moisture, Temperature, and Salinity Meter (accuracy ± 2%) inserted ~15 cm to the right of the egg chamber when facing the dune face so that measurements closely reflected the moisture content of the nest without puncturing any eggs with the meter. Before each use, the probe end was submerged in water and calibrated to 100% moisture. After calibration, the probe was inserted into the ground and readings were taken at the surface, 20 cm, and 40 cm below the surface. Moisture was averaged over these depths for a mean moisture content on each sample date. I measured moisture content in each nest every 10 - 16 days throughout incubation, so that the moisture of each nest was measured at least 4 - 5 times during the season. Moisture readings were always taken between 06:00 and 09:00 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 for each nest during its incubation (Lolavar and Wyneken 2017).

For the duration of the nest incubation, nests were visually inspected daily. In addition to noting any signs of nest depredation, by monitoring daily, I also recorded if the tide reached or washed over the nest during the previous night's tidal cycle. If large amounts of wrack were deposited over the nest by tides, it was removed by hand. Similarly, if large amounts of sand buildup occurred on top of the predator screen, it was removed by hand according to protocol set in place by the Georgia DNR. Nests were inspected and maintained daily until predation, hatching crawlways were found, or until 70 days after the nest was deposited. Once hatchling crawlways were observed leaving a nest, the nest was marked as hatched, and the nest was inventoried five days later. If no signs of hatchlings were observed by day 70 of incubation, the nest was opened and inventoried, since this is an indication that no eggs will successfully hatch (Dodd and Raybould 2014).

Nest Inventory and Processing

During nest inventories, I removed the entire contents of the nest, and counted all hatched and unhatched eggs. Any live hatchlings found in the nest at the time of inventory were allowed to crawl to the ocean by themselves. During the 2018 field season, after the inventory was completed, all unhatched eggs were opened and assessed for development using stages described by Miller et al. (2017). Initially eggs were categorized as fresh, rotten before stage, rotten beyond identification, or partially developed. Eggs were categorized as fresh if the appearance was akin to a freshly laid egg (*eg.* yolk is undeveloped and wet, no white spots, and no blood spots have formed, Figure 4a) which indicates an unfertilized egg (Miller et al. 2003). Eggs were categorized as rotten before stage if there was no visible sign of an embryo but the yolk appeared solid or decomposition of egg contents had occurred (which indicates a fertilized egg that did not complete incubation) (Figure 4b). These undeveloped, rotten eggs were generally classified as early development (Miller et al. 2017). If there was visual presence of an embryo but stage of development could not be confirmed due to decomposition, the egg was categorized as rotten beyond identification (Figure 4c). If there was any visible development of an embryo, the egg was categorized as partially developed (Figure 4d). The partially developed embryos were photographed and preserved in a 10% buffered formalin solution. The photos of the partially developed embryos were used to ascribe each embryo to one of three broad categories (early, middle, and late developmental stages) based on thirty-one stages of development (Whitmore and Dutton 1985; Miller et al. 2017). The following classifications were made based on Whitmore and Dutton (1985) and Özdemir et al. (2008): early: embryos with no visible carapace, no pigmentation, ≤10 mm total length; middle: embryos with visible carapace with no pigmentation (scutes not colored), 10 - 30 mm total length; late: embryos with dark scutes present on carapace, >30 mm total length.

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 was calculated using the following equation:

$$\frac{N\,Hatched}{N\,Total} \times 100 = HS$$

Where *N Hatched* is the number of hatched eggs at the end of incubation, *N Total* is the total number of hatched and unhatched eggs at the end of incubation, and *HS* is the percent hatch success.

In order to determine which factors might affect hatch success, I used a hierarchical approach relating all measured environmental parameters to either temperature, moisture, or number of washovers, all of which are considered critical for loggerhead hatching success (Wood and Bjorndal 2000).

A generalized linear model (GLM) was run with a Poisson distribution using a log link function to explain variation in hatch success. The GLM comprised of one response variable (hatch success) with average temperature, average moisture, and number of washovers as potential predictor variables.

To identify which environmental elements most impact temperature and moisture and ultimately affect hatch success, beach morphology variables were analyzed using a multivariate principal component analysis (PCA). Because PCA is not reliable for a large number of variables (Pond et al. 1996), a select number of variables was selected based on pairwise correlations (Table 1) and variables thought to affect the physical location of nests. Latitude, dip, strike, elevation, DTL, and vegetation were included in this analysis.

Next, I selected the first three principal components because they explained 70% of the variation in the dataset (Table 2). In order to determine which factors contributed to mean temperature and moisture, I used two separate multiple regression analyses. Either temperature or moisture were the response variables, and I used the newly generated principal components (PC 1, 2 and 3, see Table 2) as the explanatory variables. Since the principle components all had significant contributions from multiple variables, I also ran multiple regression analyses with temperature and moisture as response variables and beach morphology variables as potential predictor variables. This was done in an attempt to parse out which variables most influence temperature and moisture within each principal component from the PCA.

The number of washovers was non-normally distributed, so a GLM with a Poisson distribution and log link function was constructed to identify factors contributing to the number of times a nest was washed over. The GLM used washovers as the response variable with potential washover factors as the three principal components from the beach morphology PCA.

All data were analyzed using JMP v. 13 (SAS Institute, Cary, USA). Although all data were not able to be collected for each of the sampled nests, they were used in subsequent analyses whenever possible. The rejection level was α=0.5 for all statistical tests.

CHAPTER 3

RESULTS

During the 2017 nesting season, the first nest was laid on May 8, and the final nest was laid on July 31. During this season, 89 nests were sampled (Figure 1; Appendices 1-4). Hurricane Irma hit Ossabaw on September 10-11, 2017, and washed away 11 nests that remained incubating. All personnel were evacuated from the island on September 8, 2017, which was the last day in the season which nests were monitored. While it is possible that some of the remaining nests had successful hatchling emergences before the hurricane made landfall, it was impossible to discern after personnel returned to the beaches. Upon returning to the beaches on September 15, 2017, all primary dunes and vegetation had been washed away and none of the nests remaining before Hurricane Irma were visible. An additional 9 nests were lost due to depredation by either feral hogs (*Sus scrofa*) or raccoons (*Procyon lotor*).

The first nest of the 2018 nesting season was laid on May 15, and the final nest was laid on August 3. During this season, 111 nests were sampled (Figure 1; Appendices 5-8). By the time monitoring began in 2018, the majority of primary dunes had rebuilt following Hurricane Irma with mostly grasses, sedges, and herbs having re-established since being wiped out completely in September, 2017 (*personal observation*). Of the 111 nests initially sampled, 9 were lost due to hog and raccoon depredation, resulting in 102 nests used in the analysis.

Between 2017 and 2018 field seasons, 200 total nests were initially identified for this study. However, by the end of incubation, a total of 170 inventoried nests had a discernible hatch success and were used for subsequent analysis. Hatch success ranged from 0 - 99.2% (number of hatched eggs per clutch ranged from 0 - 134) with an average of 46.2% (SD±37.8) hatch success (Figure 5). Of these nests, 47 (27.6%) had no hatched eggs.

The average temperature for all nests was 29.73℃ (SD±0.87). In nests producing at least one hatchling (HS>0%), temperatures were measured as low as 23.96℃ in the coolest nest and as high as 35.22℃ in the warmest nests. Many nests incubated completely within the optimal temperature range of 26.5 - 32℃ (N=62). However many nests remained successful even after incubating for hours outside of the acceptable temperature range. For example, two nests incubated during the 2018 season experienced temperatures above 32℃ for 588.5 and 583 hours but were both successful with hatch successes of 88% and 96.6% respectively.

Average moisture throughout incubation ranged from 5.4 - 89.6% with an average of 49.3% (SD±18.1). Nests with average moisture at either extreme of the range produced some hatchlings. One nest which had an average moisture 89.6% had an 81.9% hatch success. Two nests on the opposite end of the spectrum with 5.4% and 8.5% moisture had hatch successes of 21.0% and 1.8% respectively.

Tidal washover and/or inundation affected 70 nests (41.2%). Of nests that experienced a tidal event, a large percentage only experienced one or two events throughout incubation (26% and 14% and respectively) (Figure 6). Beyond 6 washover events, generally no hatch success occured. However in two instances, washovers of 7 and 8 times resulted in hatch success greater than 0 (45.3% and 0.97% respectively) (Figure 7).

Vegetation was found around the majority of nests (54.7%; N=93) at some point while eggs were incubating. The percent cover of vegetation within those 93 nests ranged from 1.5 - 87.5%. The majority of vegetation surrounding nests were classified as grasses followed by sedges, and flowers and herbs being the least abundant (Table 3).

Nest elevation ranged from 1.44 - 4.25m above sea level (Figure 8) with a mean elevation of 2.09m (SD±0.37). Dip and strike were measured for 168 nests. Strike ranged from 0 - 350°

with the majority of nests striking 1 - 89° (*ie*. Northeast-Southwest). The distribution of dips measured ranged from 00 - 22° with the majority of dip direction classified as dipping SE. Overall the dips of dunes where nests were laid were gently sloped with an average dip of 06° (SD±05).

Hatch success correlated with a large number of variables (notably temperature, moisture, elevation, vegetation), and many environmental variables correlated with temperature and moisture (Table1). The beach morphology PCA (Figure 9) supports a 3-factor structure of nest latitude, strike, dip, elevation, DTL, and vegetation (Table 2). The variables which contributed to PC1 (factor loadings ≥0.40) were latitude, dip, and elevation which contrasted with strike. PC1 is loaded heavily (factor loadings ≥0.60) on higher nests with steeper slopes striking to the NE (1-89°). The variables which contributed to PC2 (factor loadings ≥0.40) were strike, DTL, and vegetation which contrasted with latitude. PC2 is heavily loaded (factor loadings ≥0.60) on vegetation across a latitudina l gradient; nests deposited farther southward have more vegetation. The variables which contributed to PC3 (factor loadings ≥0.40) were DTL and vegetation. PC3 is heavily loaded (factor loadings ≥0.55) on increased vegetation as nests are located farther away from the tideline and closer to dunes. Together these three components account for 69.8% of the variation seen in the data (Table 2).

Principal Components 1, 2, and 3 were all found to be significantly correlated with the average temperature in the nest. Only PC2 was found to be significantly correlated to average moisture. (Table 4). Multiple regression analysis with temperature as a response variable indicated that vegetation and elevation correlate positively with temperature and explain 37% of variation in nest temperature (Figure 10). For every increase in nest elevation by 1 m, average nest temperature increases by 1°C (Figure 11a). Similarly, as average vegetation cover increases in 20% increments, average nest temperature increases by 0.5°C (Figure 11b). Multiple regression with moisture as the response variable using individual beach morphology variables as potential predictor variables yielded elevation, vegetation, DTL, and strike as significant factors affecting moisture and explain 18% of the variation (Figure 12). Most notable was elevation (p=0.0045) whereby moisture decreased by 10% per increase of nest elevation by 1 m (Figure 13a). Vegetation, DTL, and strike were also important in explaining variation in moisture. Moisture significantly decreased (p=0.0124) as more vegetation was present (Figure 13b). Moisture also decreased significantly (p=0.0166) the farther away a nest was placed from the tideline (Figure 13c). Moisture generally decreased as strike increased (p=0.0268) where nests placed on dunes that strike to the NE-SW had more moisture than those dunes that strike SE-NW, N-S, or E-W (Figure 13d; Appendices 9-16).

The GLM with number of washovers as the response variable indicated that principal components 1, 2, and 3 were all significant in explaining the number of tidal events a nest experienced (Table 5).

The GLM with hatch success as the response variable indicated that temperature, moisture, number of washovers, and all combinations, were significantly correlated to hatch success. However, both washovers ($\chi\chi^2 = 1102$) and nest temperature ($\chi\chi^2 = 781$) seemed to have the strongest effects on hatching success (Table 6).

Embryo Mortality

A total of 5,718 unhatched eggs from 88 nests incubated in 2018 were opened. Of these, 4,232 were assessed as early, middle, or late stage of development. The remaining 1,486 were classified as rotten beyond identification (N=1,164), unfertilized (N=194), or unknown (N=128). Fertility was 97.98% for the 88 nests assessed in 2018.

The largest percent of nest mortality occurred in early stage embryos followed by late stage embryos with a very small percentage of nest mortality occurring in the middle stage of embryonic development (Figure 14). The average percentage of early stage development eggs was 45% (SD±32; N=88) per nest. The average percentage of middle stage development eggs was 4% (SD±10; N=62) per nest, and the average percentage of late stage development eggs was 27% (SD±31; N=77) per nest. A larger percentage of late stage development eggs were found in nests laid at the beginning of the season and decreased as the season progressed.

Inversely, the percentage of early stage development eggs per nest increased as the season continued (Figure 15). Each stage of development had some significant correlation with incubation temperatures inside the nest (Table 7).

Hatchling Sex Ratios

Hatchling sex ratios were estimated based on the average temperature during the middle third of incubation (Standora and Spotila 1985; Kaska et al. 1998) using the equation for hatchling sex ratio in LeBlanc et al. (2012). Of the 170 nests included in this study, 47 had 0% hatch success which made it impossible to determine the average temperature during the critical or thermosensitive period (middle third of incubation) which is needed to estimate hatchling sex ratios. Additionally, some of the remaining nests had datalogger malfunctions resulting in 118 nests with discernable critical period temperatures. The average temperature for these nests during the critical period was 29.87°C (SD±0.90). Over the 2017 and 2018 nesting seasons, average males estimated per nest was 24.4% (SEM±1.69), and average females estimated per nest was 75.6% (SEM±1.69), and there were no male-biased nests in 2018 (Table 8).

CHAPTER 4

DISCUSSION

Temperature, moisture and tidal inundation have long been known to drastically affect hatch success in sea turtle nests (Carthy et al. 2003; Tuttle and Rostal 2010; Ditmer and Stapleton 2012; Brig 2014; Lolavar and Wyneken 2015; Hays et al. 2017). Many studies have analyzed nesting conditions and their effects on eggs in laboratory settings with constant variables like moisture and temperature (Bull and Vogt 1979; Dutton and Whitmore 1984; Georges et al. 1994; Fisher et al. 2014). These studies have offered valuable insight to development and the success of the nest, but few measure these variables *in situ* and attempt to explain variation in these variables by measuring a suite of other environmental parameters.

For my study, all three major environmental variables affected the hatching success of loggerhead turtles, although temperature and number of tidal washovers may have a stronger effect. In addition, many variables measured in this study correlated with hatch success such as percent cover of vegetation, nest elevation, and nest dip. However, by using a hierarchical approach, I was able to explain some of the variation in temperature, moisture, and frequency of tidal washovers as they are impacted by other environmental variables. In particular, elevation and vegetation cover were important drivers of the three factors generally considered most important for hatching success, although further exploration is necessary.

Mean nest temperature had a strong, positive relationship with hatching success, such that as temperature of the nest increased, so did the number of successfully hatched eggs. This is not surprising, since temperature controls embryo development (Bull and Vogt 1979; Bull 1980) and the average nest temperature in this study was well within the accepted optimal range of 26.5-32°C. Further, nests rarely consistently experienced temperatures outside the optimal range in this study, and few nests exhibited average temperature near the two ends of the range. My study supports findings from other studies (Carthy et al. 2003; Ditmer and Stapleton 2012) that hatch success increases as temperature increases. Other studies have reported a decreased hatch success (*eg*. Hays et al. 2017) if incubation temperatures exceed temperatures 31.5°C. Similarly some studies have indicated that nests with warmer temperatures experience lower hatch success (Lolavar and Wyneken 2015; Kobayashi et al. 2017) with some nests experiencing temperatures of 36-37°C toward the end of incubation. In this study, average temperatures never reached 32°C, so the positive correlation of hatch success with temperature holds true when nests do not incubate at average temperatures above 32°C (Fisher et al. 2014).

Nest temperature was consistently impacted by vegetation and elevation such that warmer nests had more vegetation and were placed at higher elevations. Vegetation was more common around hotter nests indicating that it does not provide cooling effects. However this effect could change if vegetation composition consisted of more broad-leaved species instead of the narrow-leaved species of grasses and sedges (Ferreira Júnior et al. 2008; Brantley et al. 2014) which were most common on Ossabaw dunes during this study. Grasses are the first plants to establish after a major storm or tide event and facilitate the building of primary dunes (Brantley et al. 2014) which explains the composition of vegetation observed around nests on Ossabaw. Both seasons when data were collected were preceded by hurricanes (Matthew in 2016 and Irma in 2017) which majorly or entirely wiped out all primary dunes and all vegetation associated with them (*personal observation*). It may also be possible that vegetation is only found in locations farther away from the tideline in areas of high elevation. Vegetation may ultimately act as an indicator for parts of the beach where the tide doesn't often reach and where sand temperature and moisture are within ideal incubation ranges.

In addition to vegetation, the elevation of a nest directly impacted the temperature. In the face of predicted climate change, it is possible that nests at higher elevations may experience temperatures outside of the optimal range. However, it is likely that elevations will change with predicted climate change and sea level rise, which will likewise alter beach morphology and loggerhead nesting habitat (Brantley et al. 2014). It has been suggested that in the face of a changing climate, sea turtles may undergo a phenologica l shift by nesting at different elevations (Hawkes et al. 2007). Because the nests in this study were left *in situ*, it may be possible that turtles naturally place nests where incubation temperatures will not exceed lethal limit temperatures especially given that few if any nests in this study at high elevations exceeded the thermal limit. However this could change if nesting beaches experience drastically higher air temperatures, more precipitation, or other factors that would drastically change sand temperatures from the time to nest site selection and throughout incubation. Similarly, steeper nests—those with larger dips—were warmer. This may be due to those sloped nests experiencing sun radiance for longer periods of time than those nests which have little or no slope (R. Kelly Vance, *personal communication*; Lavallin 2015). Likewise, more sloped nests generally had higher elevations leading to an increase in nest temperature.

Moisture was most influenced by elevation, vegetation, DTL, as well as the strike of dunes. Nests with more vegetation, higher elevation, and farther away from the tideline were drier. Nests with higher elevations tend to incubate at higher temperatures leading to a decrease in nest moisture as evaporation occurs and as the likelihood of washovers is decreased (Foley et al. 2000; Lavallin 2015). It is also possible that the nest's distance from the water table has a significant impact on temperature (Lavallin 2015). These high nests are also less likely to experience tidal events which contribute to increased moisture in the nest. The negative relationship between vegetation and moisture indicates that the grass and sedge species are wicking away moisture from around the nest substrate. Dune morphology in the form of strike impacts nest moisture in that nests on host dunes that strike to the NE-SW have generally drier nests compared to those striking to the SE-NW. This might be indicative of nests on dunes striking to the NE-SW getting more intense overhead sun for longer in the day compared to nests which strike more southerly which get the less intense afternoon sun.

The frequency with which nests experienced tidal washover was influenced by the same beach morphology variables as temperature and moisture. Most importantly washover was influenced by elevation, vegetation, DTL, and latitude. Nests placed higher up on dunes farther away from the tideline are less likely to be washed over by spring high tides and storm surge events. The presence of vegetation also decreased a nest's likelihood of experiencing a tidal washover. This may simply be an effect of vegetation increasing away from the tideline, but it may also be possible that sand builds up around vegetation (Brantley et al. 2014) over the course of incubation effectively creating mini-dunes around nests which may buffer some tides (*personal observation*). What was interesting was the latitudinal gradient of washovers that increased as nests were placed farther north on the island. It may be possible that the northern end of the island experiences washovers more frequently due to an increased number of washover fans on low areas of beach and increased vegetation on the south end of the island (Gale Bishop, *personal communication*). These washover fans are occurring as transgression of beaches occurs, pushing back the shoreline as a result of rising sea levels (Bishop etal., *unpublished data*).

Tidal inundation and washover has consistently been cited as a factor that decreases hatch success in marine turtle nests (Wood and Bjorndal 2000; Foley et al. 2006; Brig 2014). All nests in this study were left *in situ* reflecting the natural nest site selection by females. About 59% of nests (N=100) were never washed over indicating that turtles might select sites based on likelihood of washover. It should be noted that one nest in this study experienced 7 washover events and yielded a hatch success of 45.3% suggesting that there are other factors within the nest environment that may combat the effects of successive washovers. Specifically this nest had an average elevation (2.1 m) and an above average dip of 10°. This slope of the dune may have helped the nest and surrounding substrate drain after washovers. While most nests can withstand minimal tidal inundations and washover without drastic impacts on hatch success, nests at low elevations more frequently inundated by tides experience low hatch success (Foley et al. 2006; Brig 2014). One study conducted on low-relief mangrove islands, which are physically different habitats from those of barrier islands, showed that high moisture was a significant contributing factor to lower hatch success only when tidal inundation occurred (Foley et al. 2006). This appears to hold true in this study as tidal inundation and temperature have seemingly more influence on resulting hatch success than does moisture. In this study, hatch success decreased exponentially with subsequent washovers experienced by a nest. This indicates that the relocation of nests may only be necessary when tidal inundations are likely to be frequent throughout incubation.

Because of the patterns of daily and seasonal temperature and moisture fluctuation, studying nest conditions *in situ* is vital in understanding how a collection of environmental variables impact hatch success. Analyzing biotic and abiotic environmental variables of beach morphology at the nest site indicates how these variables affect temperature, moisture, and washover events which is especially important because many of these variables are studied as singular variables or are grouped with one or two other environmental variables to explain hatch success. These trends can be extrapolated to generally determine how combinations of these environmental factors are related to temperature, washovers, and moisture and in turn how they impact hatch success.

The higher rates of embryo mortality seen in early and late stages of embryo development compared to middle stages has been reflected in other mortality studies (Özdemir et al. 2008; Ilgaz et al. 2011). The increase of early stage mortality and decrease of late stage mortality as the season progressed (Figure 15) could potentially be linked to some environmental phenomenon which rendered development impossible. It is possible that a sudden temperature drop and moisture increase as a result of heavy precipitation events could halt development in many nests. Eggs laid in May that would have been in the last stages of development would have been inventoried shortly after this series of rain. Similarly eggs that had been laid just before or during this period in June (when the nesting events reach their peak on Ossabaw (GADNR, *unpublished data*)) would have stopped developing early and would not have been inventoried until the 70 day mark toward the end of the season. This idea could be analyzed more in depth to determine how closely nest temperature drops coincided with individual rain events. However this would not explain why nests laid after these precipitation dates continued with the same trend. The trends in egg mortality may be more largely influenced by some other environmental variable, and should be explored further.

While not considered for environmental factors affecting hatch success, maternity could be an additional factor which influences nest hatch success (Ditmer and Stapleton 2012). Of the 170 nests used in this study, 160 have been assigned maternity through maternal DNA present in freshly-laid egg shells (Shamblin et al. 2011). These 160 nests were laid by 106 unique females. Of these, 24 were individuals that had not been identified through the Northern Recovery Unit

(NRU) Loggerhead DNA genetics project in the years previous (beginning with the genesis of the project in 2008) to the nesting season that they were active, so they were assumed to be neophytes recruiting to the breeding population for the first time. The remaining 82 individuals were remigrants that had nested in the area previously based on genetic sampling of eggs which began in 2008. Hatching success was higher in the neophytes than in the remigrant individuals (Wilcoxon rank-sum tests, N=30, 130; p=0.0218) (Appendix 17). The nesting grounds included in the NRU are Georgia, South Carolina, and North Carolina with sporadic samples from Virginia and rarely more northern states when turtles nest there.

Many loggerhead nesting grounds are estimated to produce female-biased sex ratios (Kaska et al. 1998; Foley et al. 2000). Ossabaw Island produces female-biased incubation conditions in *Caretta caretta*. Foley et al. (2000; 2006) suggest that there is a natural nesting pattern that combats hatchling sex-bias when nests are left *in situ* and that relocation should only be considered for nests which are highly likely to experience complete loss. Male loggerheads appear to mate more frequently than do females thereby increasing their operational sex ratio to be about 50:50 male:female even though most populations have a female bias (Hays et al. 2010). Because of this operational sex ratio, the increase of female-biased beaches helps loggerhead populations increase. However if temperatures continue to increase and reach or exceed upper lethal limits, it may be beneficial to leave more nests *in situ* to avoid a complete female bias and increased rates of hatchling mortality due to incubation temperatures exceeding lethal limits.

The management of *Caretta caretta* for increasing nesting populations begins with managing nests for increased hatch success. There are many factors which may influence the success of a nest, and most of these variables are dependent on others. While nest temperature, likelihood of tidal washover, and moisture are important predictors of hatch success, other environmental variables interact with each other to influence the aforementioned variables. In order to achieve warmer temperatures and decreased moisture, it may be necessary to relocate nests in order to avoid tidal washovers. The findings here support relocation to higher dunes where vegetation is present in order to influence temperature and moistures. This study also indicates that the presence of vegetation is a good gauge of a location which will be conducive to high hatch success. Relocating nests to elevations which correlate with a specific average temperature and moisture associated with high hatch success could increase the success of the nest. However dunes of high elevation may not be available on all nesting beaches due to natural factors (eg. tidal washover fans, loss of dunes due to storm events) or man-made factors (eg. sea walls) (Wang and Horwitz 2007; Bishop et al., *unpublished data*). If these dunes are not present or if seasonal temperatures are expected to be too hot for successful incubation, simply relocating a nest farther away from the tideline may be significant enough to increase hatch success.

In addition to consideration of elevation and DTL, vegetation cover and composition should be considered as a variable which influences the success of a nest. Although vegetation composition and cover may change throughout incubation (as observed in this study), relocating a nest nearby presently existing vegetation may increase nest temperature which would be desirable in certain nesting seasons where temperatures are expected to be lower than average or heavy rains are expected to decrease sand temperatures. The slopes of dunes could be an important factor to consider when relocating as well as dunes with steeper slopes have better drainage (decreased moisture) and may experience warmer temperatures more suitable to successful incubation.

The interconnectedness of temperature, moisture, tidal washover, elevation, vegetation, dip, strike, and distance to the tideline make all of these variables important to some degree in predicting hatch success. By understanding how these variables change the incubation environment, managers for this species can better predict not only how successful a nest will be but can also make educated decisions when considering nests for relocation to increase hatch success. This study upholds similar findings from other research such that warmer temperatures with less moisture increase hatch success and have significant impacts on the success of the nest. The consistent instance of vegetation occurring with nests that have higher temperatures and lower moisture indicates that the presence of vegetation should be used as an identifier for locations that have conditions which result in high hatch success. When relocating nests, moving nests to dunes farther away from the high tideline that have vegetation is the best way to place nests in locations where high hatch successes are more likely.

Table 1. Significant pairwise correlations between hatch success (HS), temperature, moisture, and other environmental variables measured throughout incubation. Distance from tideline (DTL).

Parameters	**Spearman ρ**	**Probability> |ρ|**
HS * dip	0.2645	0.0005
HS * elevation	0.5549	<0.0001
HS * vegetation	0.5087	<0.0001
HS * moisture	-0.2227	0.0036
HS * # washovers	-0.5597	<0.0001
HS * temperature	0.6069	<0.0001
HS * hours outside temperature range	0.2263	0.0030
Temperature * dip	0.1743	0.0239
Temperature * elevation	0.5529	<0.0001
Temperature * vegetation	0.5060	<0.0001
Temperature * moisture	-0.5112	<0.0001
Temperature * # washovers	-0.3783	<0.0001
Moisture * strike	-0.1769	0.0222
Moisture * elevation	-0.2260	0.0037
Moisture * vegetation	-0.3562	<0.0001
Moisture * DTL	-0.1540	0.0457
Moisture * # washovers	0.3053	<0.0001

Table 2. Factor loadings for factors related to beach morphology of the nest site.

Parame ter	**PC1**	**PC2**	**PC3**
Latitude	**0.42**	**-0.68**	0.20
Strike	**-0.60**	**0.45**	0.07
Dip	**0.75**	0.09	0.11
Elevation	**0.74**	0.35	0.14
Vegetation	0.07	**0.68**	**0.57**
Distance from tideline	0.38	**0.49**	**-0.70**
Percentage of variation	29.9	24.9	15.0

Table 3. Composition of vegetation surrounding nests at time of inventory. N=62.

	Grasse s	**Se dge s**	**Flowers and Herbs**
No. of nests	46	30	8
(%)	74.2	48.3	12.9

Table 4. Multiple regression summaries using principal components (PC) from nest site parameters for nest variables average temperature and average moisture.

Parameter	t Ratio		Probability >|t|
Temperature			
PC1	**3.95**		0.0001
PC2	**5.86**		<0.0001
PC3	**5.65**		<0.0001
F		**27.24**	
P		**<0.0001**	
R^2		**0.34**	
Moisture			
PC1	-1.50		0.1358
PC2	**-4.22**		<0.0001
PC3	-0.48		0.6319
F		**6.71**	
P		**0.0003**	
R^2		**0.11**	

Table 5. Summary of GLM parameter estimates fitted to number of washovers.

Parameters	**L-R X^2**	**Probability > X^2**
PC1	109.6	<0.0001
PC2	150.6	<0.0001
PC3	39.71	<0.0001

Table 6. Summary of GLM parameter estimates fitted to hatch success.

Parameters	**L-R X^2**	**Probability > X^2**
# washovers	1102	<0.0001
Temperature	781.3	<0.0001
Moisture	279.9	<0.0001
# washovers * temperature	264.7	<0.0001
Moisture * # washovers * temperature	121.5	<0.0001
Moisture * temperature	100.2	<0.0001
Moisture * # washovers	96.63	<0.0001

Table 7. Significant pairwise correlations between percentages of embryo mortality and environmental parameters. Here early, middle, and late refer to percentages of early, middle, and late stage embryos per unhatched eggs in a nest. Day of year refers to the day of year the nest was deposited based.

Parameters	**Spearman ρ**	**Probability> |ρ|**
Early * day of year	0.3700	0.0004
Early * no. eggs incubating	-0.2235	0.0364
Early * hours below 26.5°C	-0.2149	0.0443
Middle * middle third temperature	-0.4480	0.0070
Middle * hours above 34°C	-0.2799	0.0275
Middle * hours outside 26.5-34°C	-0.3952	0.0015
Late * day of year	-0.3821	0.0006
Late * latitude	0.3141	0.0054
Late * hours below 26.5°C	0.3629	0.0012
Late * hours outside 26.5-34°C	0.2388	0.0365
Late * early	-0.6830	<0.0001

Table 8. Summary of estimated hatchling sex ratios using the average temperature during the middle third of incubation (critical period temperature) based on the formula for sex ratios as described in LeBlanc et al. (2012). In 2017, N=60; in 2018, N=58.

	2017			**2018**		
	Female		Male	Female		Male
Average % per Nest (SEM)	71.8	(2.55)	28.2	79.6	(2.10)	20.4
Median (%)	75.4		24.6	85.9		14.1
Estimated # Hatchlings	3386		1122	3096		683
Range (%)*	17.2 - 98.9		1.06 - 82.8	40.3 - 98.0		1.99- 59.7

*Range values are observed from individual nests.

Figure 1. Map of Ossabaw Island, Georgia with nest locations for 2017 and 2018 nesting seasons.

Figure 2. Image of a body pit made by a nesting female loggerhead by disturbing the topmost inches of sand with her flippers before and after eggs are deposited. *Spartina* from beach wrack outline the location of the body pit.

Figure 3. Characteristics of dip and strike as they were measured on sand dunes.

Figure 4. Image classification of unhatched eggs. (a.) Unfertilized eggs remain visibly similar to freshly-laid eggs even after 50-70 days under incubation conditions. No signs of decomposition arere present. (b.) Contents of eggs that would be categorized as rotten before stage (RBS). Yolk does not retain its liquid state and some evidence of mold and decomposition is present. No embryo is visibly present. (c.) Contents of an egg that would be classified as rotten beyond identification (RBID). Development of an embryo is clearly present (black scutes are visible on the yolk in the upper righthand corner), but the egg contents are too rotten or decomposed to identify stage of development. (d.) Eggs classified as partial had an embryo that is visible to the naked eye with no signs of decomposition or decomposition so slight that stage identification remains possible.

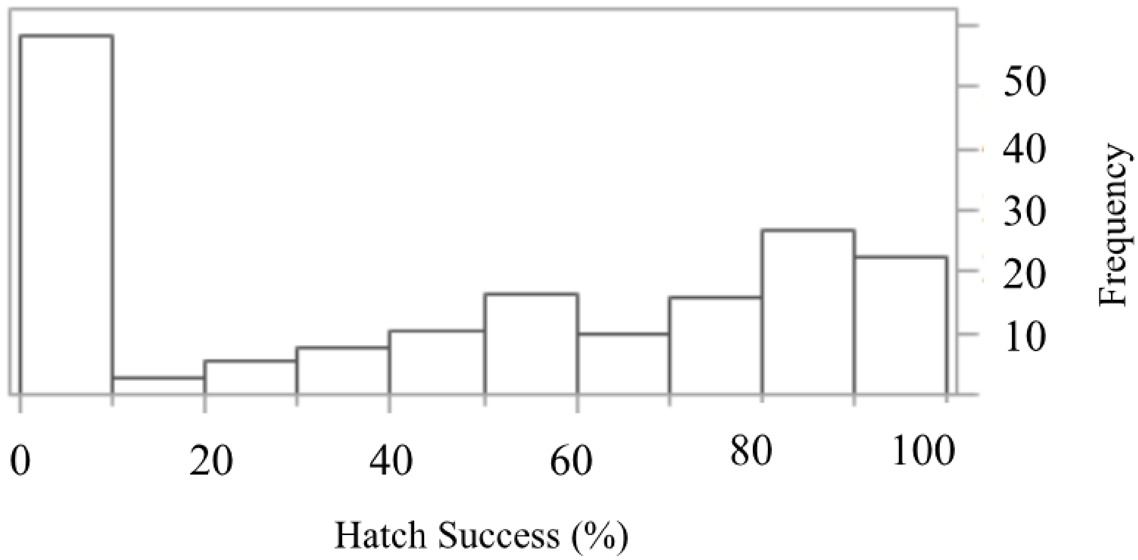

Figure 5. Distribution of hatch success (%) for nests on Ossabaw Island, Georgia 2017, 2018. N=170.

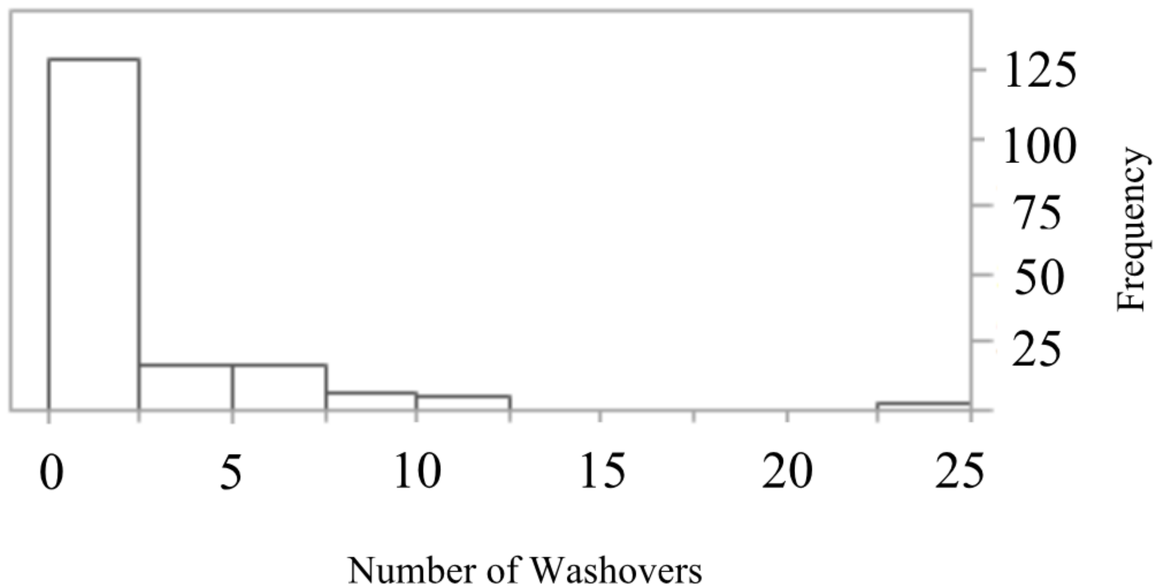

Figure 6. Distribution of tidal washover or inundation events per nest during incubation. N=170.

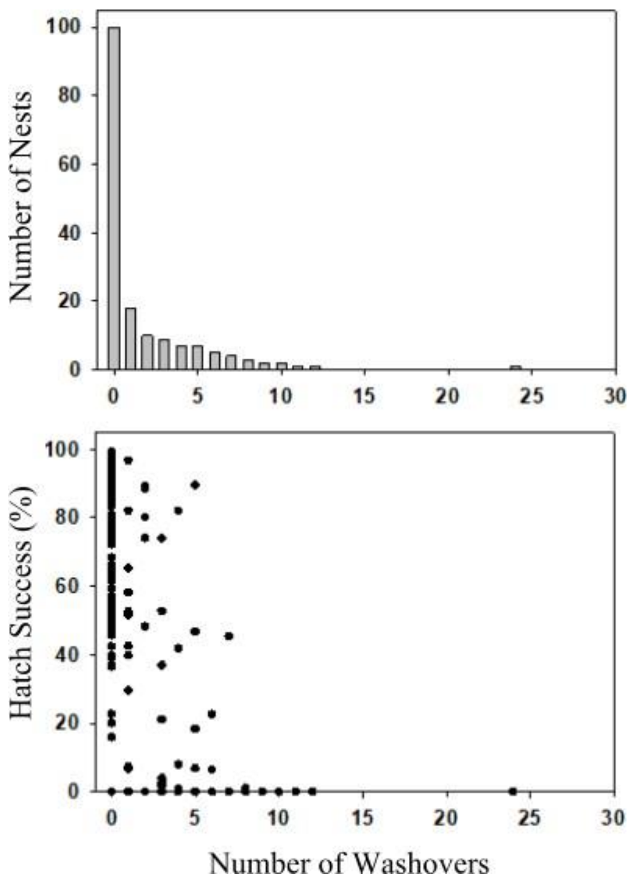

Figure 7. (a.) Distribution of frequencies of washovers experienced by individua l nests. (b.) Resulting hatch success (%) as influenced by the number of washovers each nest experienced. N=170.

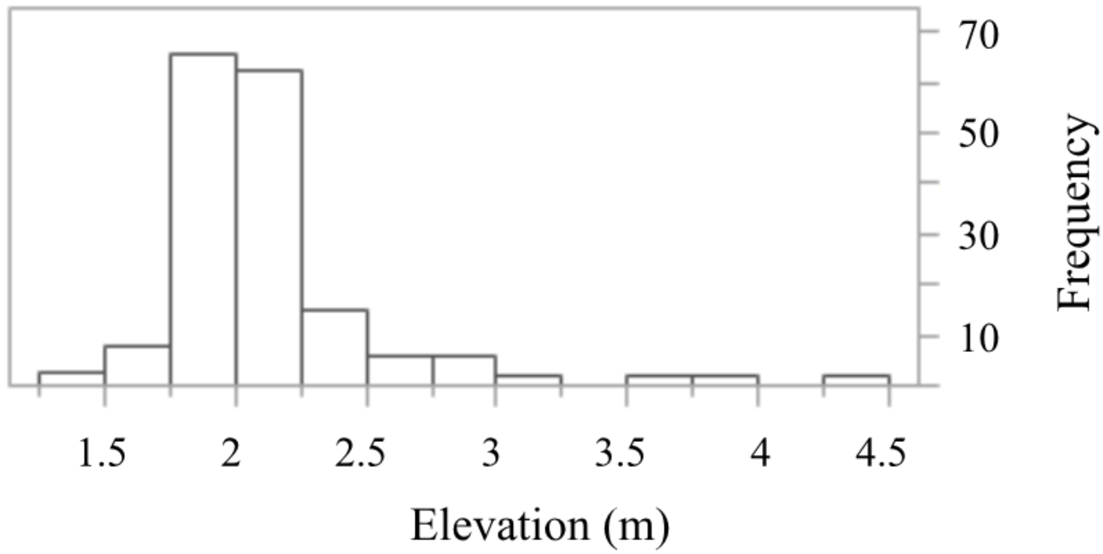

Figure 8. Distribution of nest elevation above mean sea level (m). N=164.

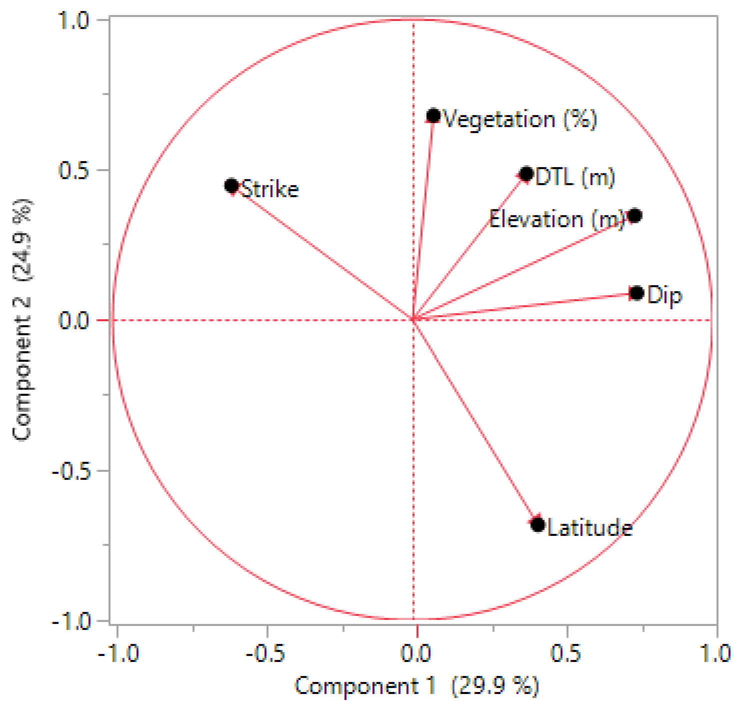

Figure 9. Ordination of beach morphology variables' scores derived from a principal component analysis (PCA).

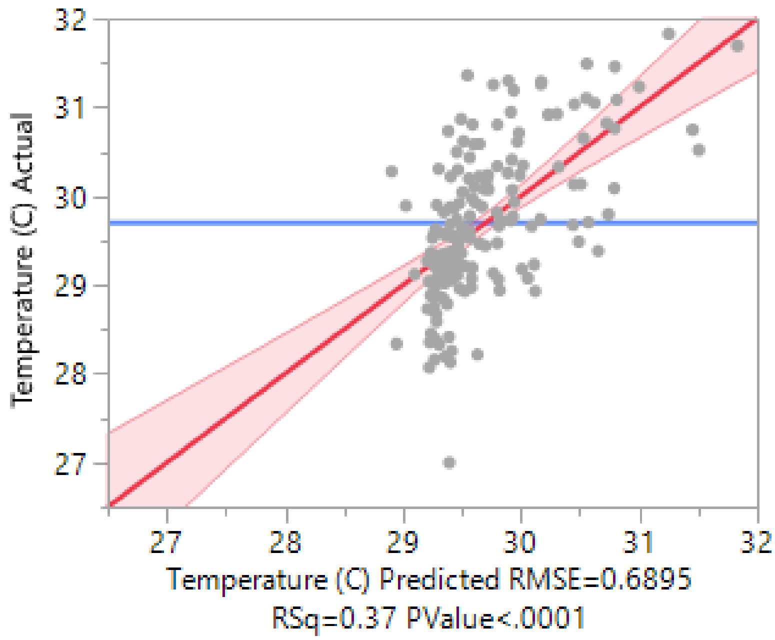

Figure 10. Multiple regression analysis with elevation and vegetation as predictor variables for temperature. N=162.

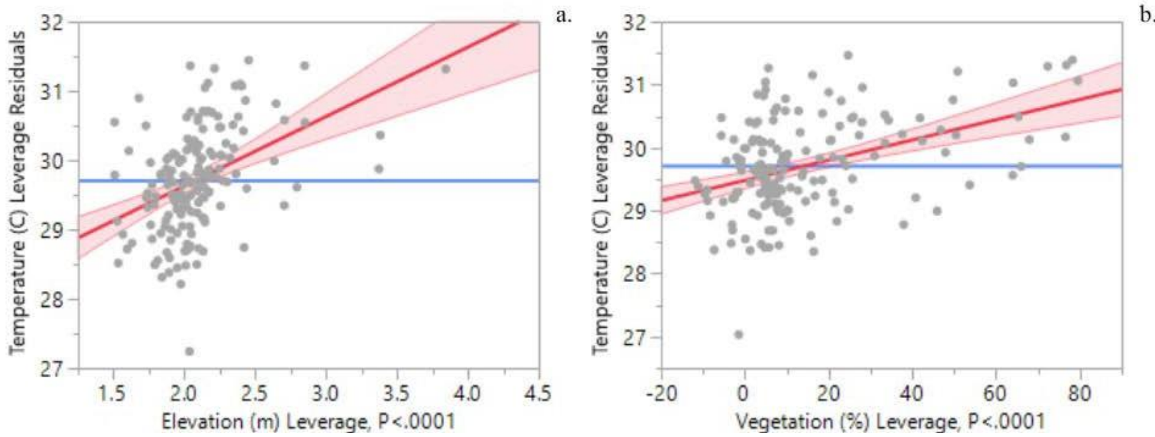

Figure 11. Multiple regression of elevation (m) above mean sea level (a.) and percent vegetation cover (b.) for nests plotted against residual temperature. N=162.

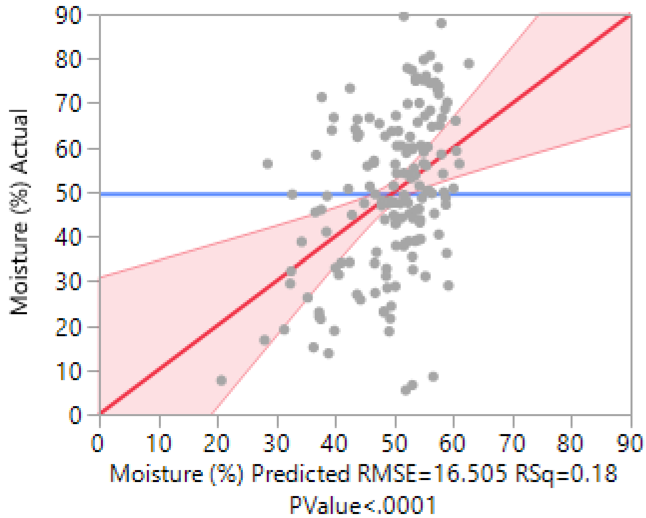

Figure 12. Multiple regression analysis with elevation, vegetation, distance to the tideline, and dune strike as predictor variables for moisture. N=161.

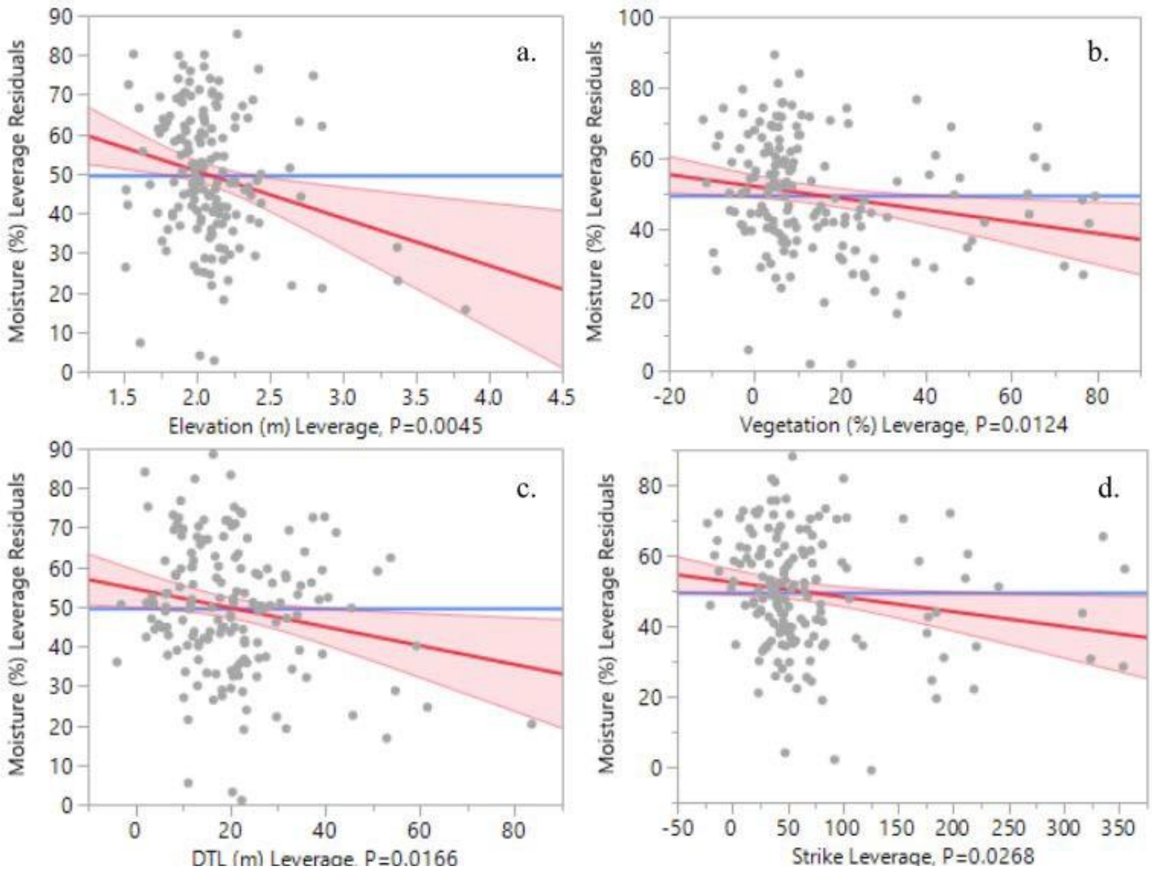

Figure 13. Multiple regression with (a.) elevation (m) above mean sea level, (b.) percent vegetation cover, (c.) nest distance to the tideline in meters (DTL), and (d.) nest strike for nests plotted against residual moisture. N=161.

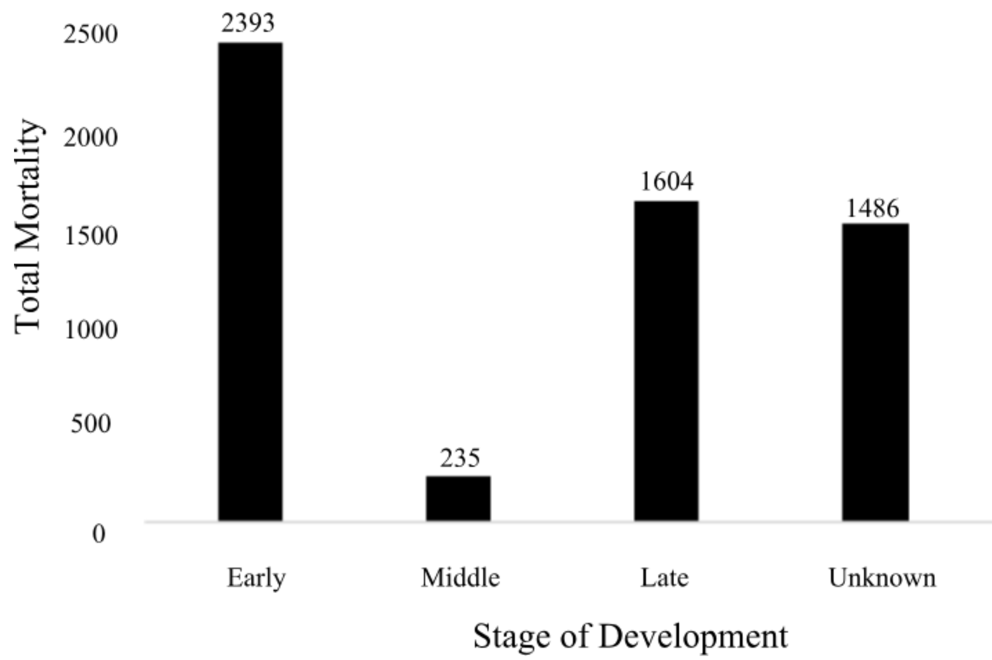

Figure 14. Total early, middle, and late stage embryo mortality from nests laid in the 2018 nesting season. N=88.

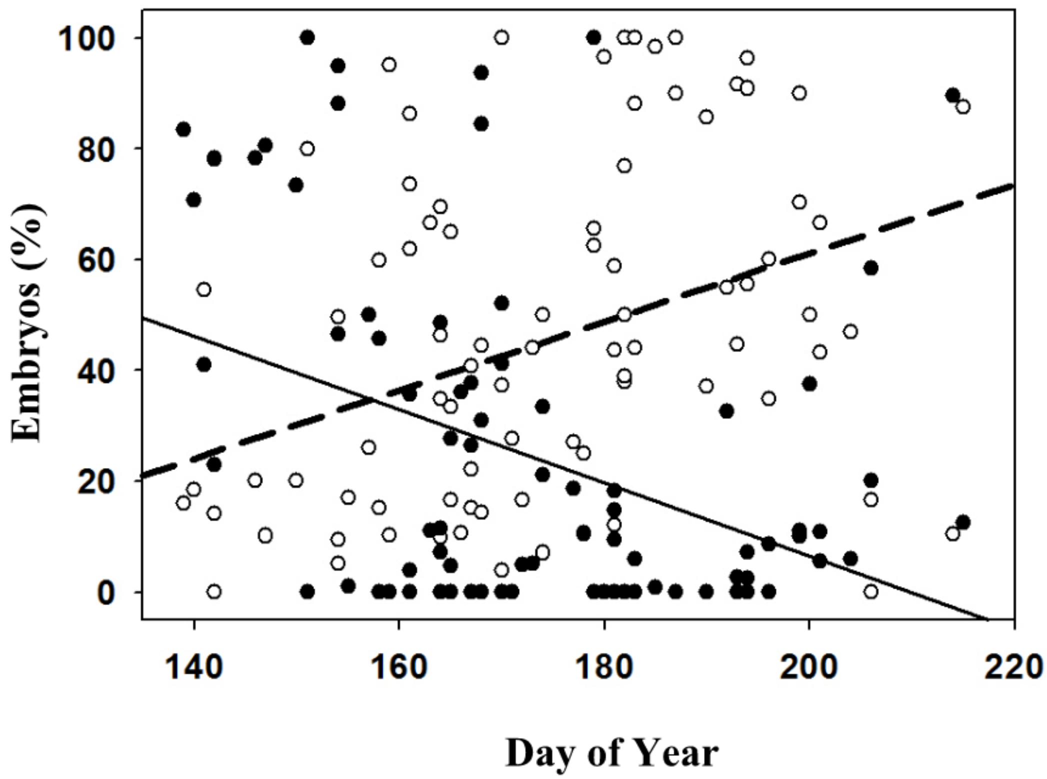

Figure 15. Percentage of early and late stage embryo mortalities per nest (N=88) based on number of unhatched eggs as they change throughout the season. Day of year refers to the Julian date when nests were deposited. Percentage of early embryos is represented by open circles; percentage of late embryos is represented by closed circles. Early stage (dashed line) = -62.4 + (0.62 *day of year) (R^2 = 0.123, p <0.001) Late stage = 138.8 + (0.88 * day of year) (R^2 = 0.152, p<0.001)

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APPENDICES

Appe ndix 1. Aerial view of Ossabaw Island with nest locations for nests incubating on North Beach during the 2017 nesting season.

Appe ndix 2. Aerial view of Ossabaw Island with nest locations for nests incubating on North Middle Beach during the 2017 nesting season.

Appe ndix 3. Aerial view of Ossabaw Island with nest locations for nests incubating on South Middle Beach during the 2017 nesting season.

Appe ndix 4. Aerial view of Ossabaw Island with nest locations for nests incubating on South Beach during the 2017 nesting season.

Appe ndix 5. Aerial view of Ossabaw Island with nest locations for nests incubating on North Beach during the 2018 nesting season.

Appe ndix 6. Aerial view of Ossabaw Island with nest locations for nests incubating on North Middle Beach during the 2018 nesting season.

Appe ndix 7. Aerial view of Ossabaw Island with nest locations for nests incubating on South Middle Beach during the 2018 nesting season.

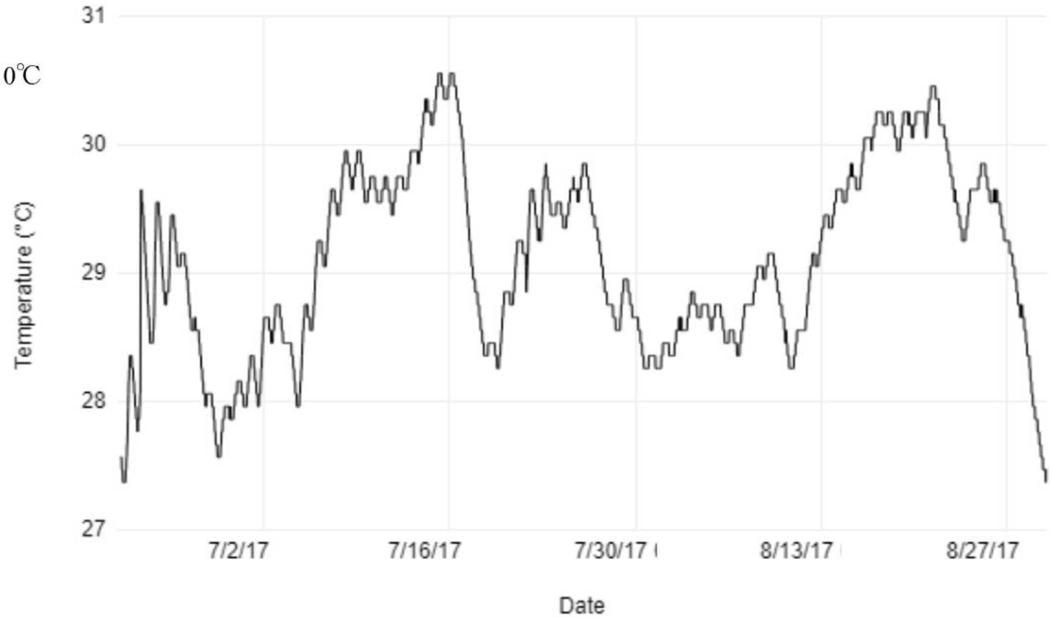
Appe ndix 8. Aerial view of Ossabaw Island with nest locations for nests incubating on South Beach during the 2018 nesting season.

Appe ndix 9. Temperature profile for NB26, 2017 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.

Nest NB44, 2017
6/7 - 8/16
019/21SE
Elevation 1.87 m
Average Temp: 28.59℃

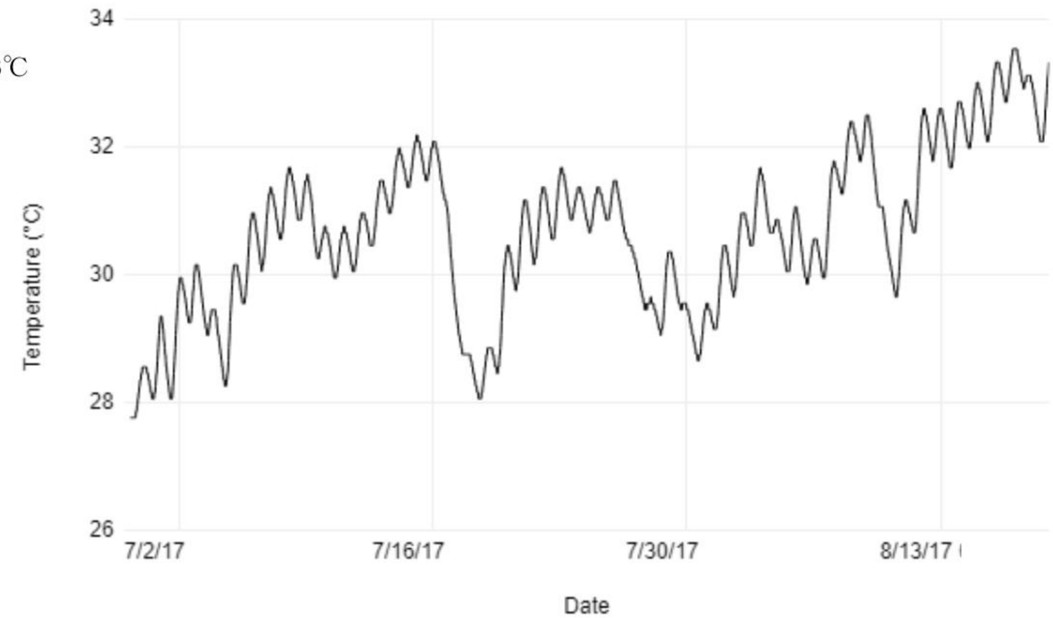
Appe ndix 10. Temperature profile for NB44, 2017 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.

Nest NB74, 2017
6/21 - 8/30
012/00
Elevation 1.89 m
Average Temp: 29.10℃

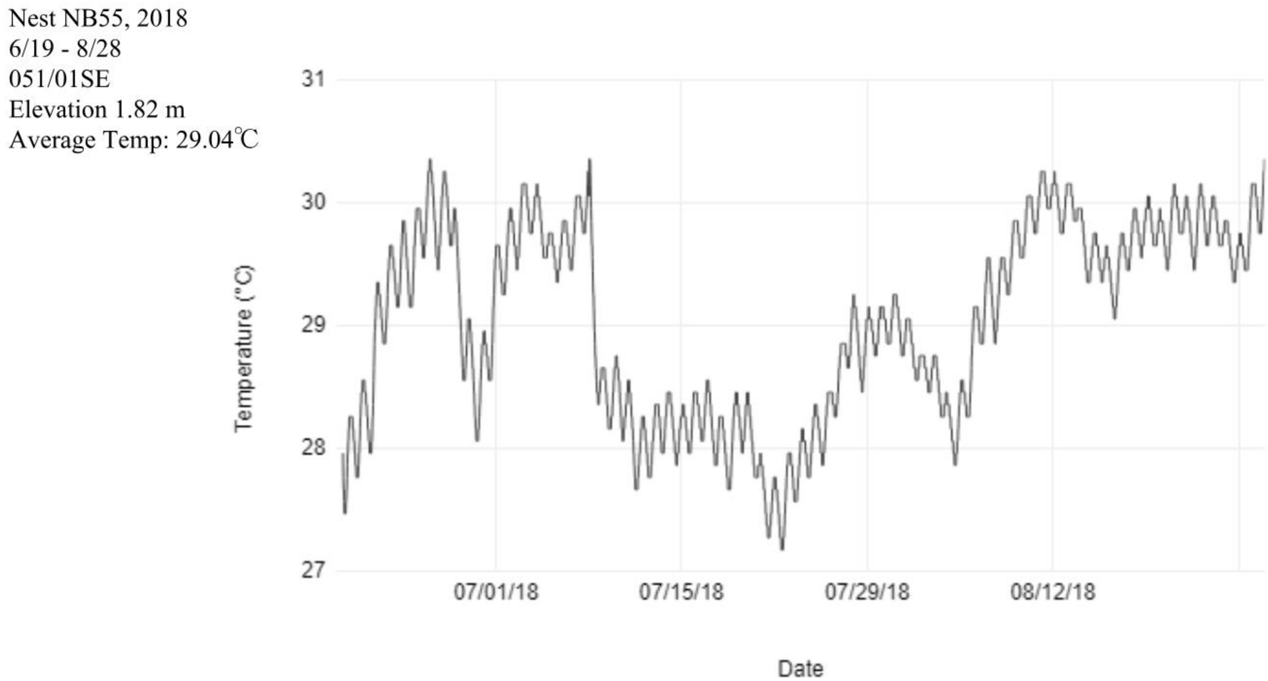


Appe ndix 11. Temperature profile for NB74, 2017 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.

Nest NM22, 2017
6/29 - 8/28
080/01SE
Elevation 1.92 m
Average Temp: 30.73℃

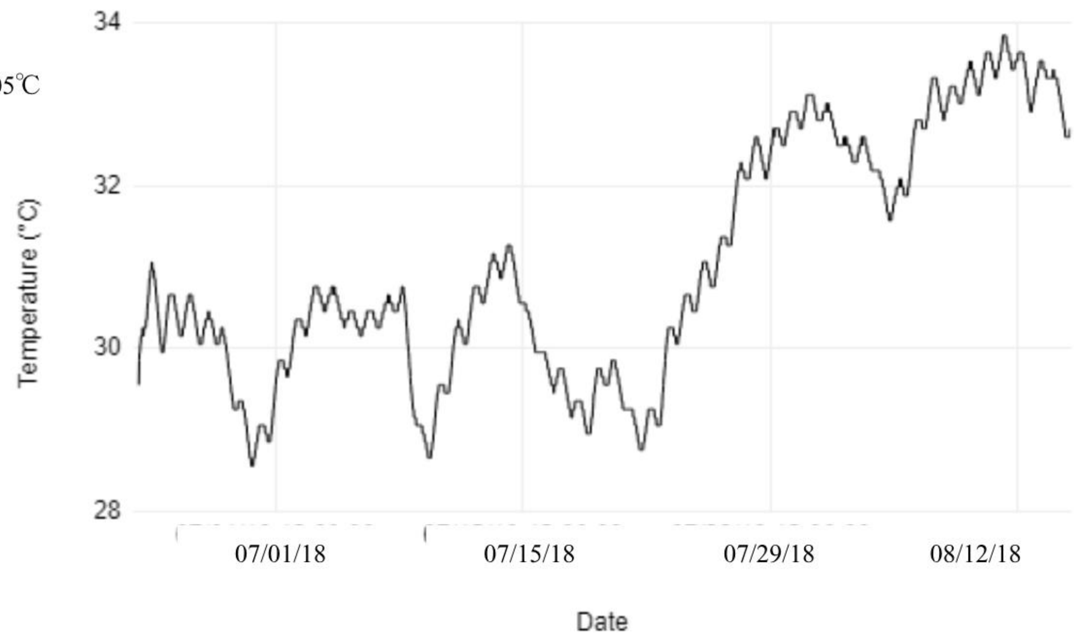


Appe ndix 12. Temperature profile for NM22, 2017 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.



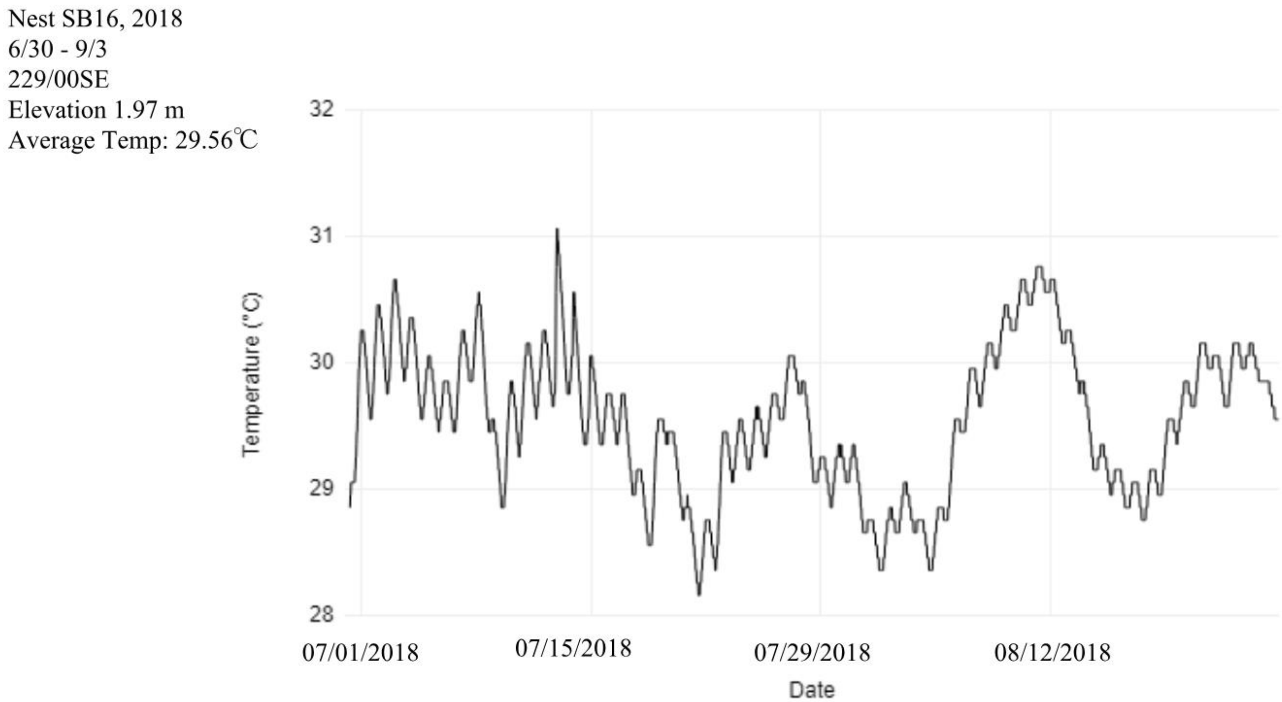
Appe ndix 13. Temperature profile for NB55, 2018 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.

Nest NB60, 2018
6/23 - 8/23
045/20SE
Elevation 2.89 m
Average Temp: 31.05℃

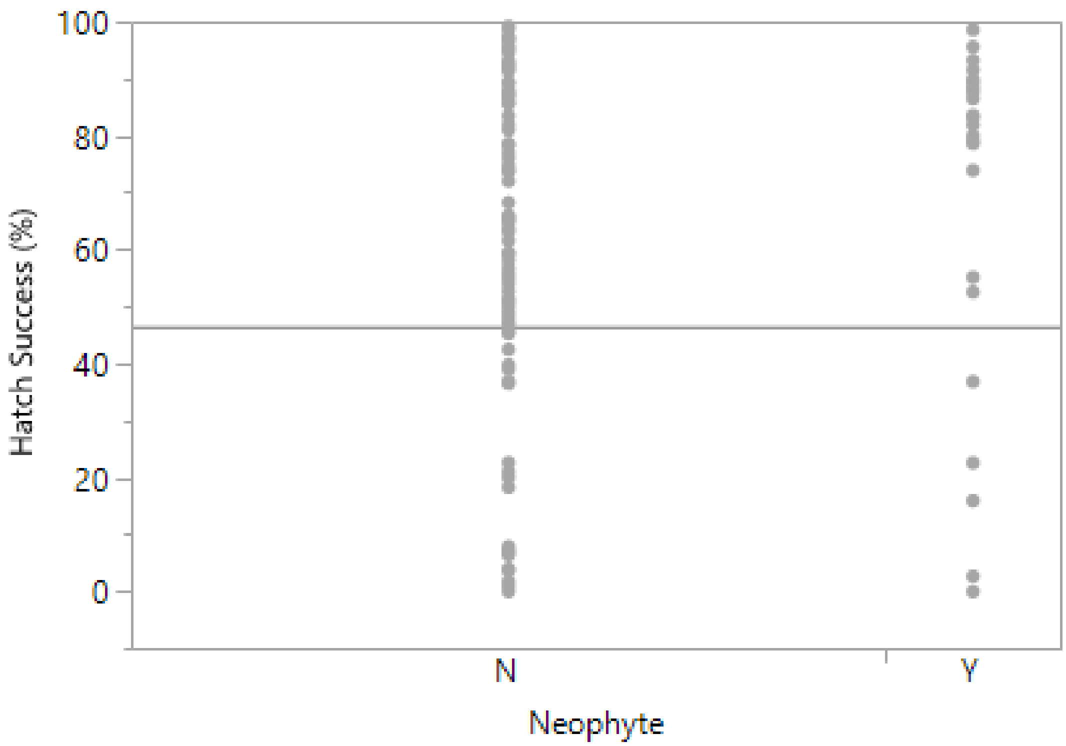


Appe ndix 14. Temperature profile for NB60, 2018 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.

Appe ndix 15. Temperature profile for SB71, 2018 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.



Appe ndix 16. Temperature profile for SB16, 2018 throughout incubation with incubation duration, strike/dip, elevation, and average incubation temperature.



Appe ndix 17. Wilcoxon rank-sum test comparing hatch success (%) in neophyte and remigrant nesters on Ossabaw Island, 2017-2018. N=30 (neophyte), 130 (remigrant); *p*=0.0218