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Thesis of
Kelly M. Detmer

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

December 2020

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Halmos College of Arts and Sciences

Using Track Widths of Loggerhead (*Caretta caretta)* Sea Turtles as a Proxy for Predicting Nesting Characteristics

By

Kelly M. Detmer

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science

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December 2020

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Abstract

Global populations of sea turtles have suffered major declines over the past century. Thus, it is critical to determine accurate demographic parameters and abundance estimates to fill current data gaps and inform effective conservation and recovery strategies. Population models with greater complexity and predictive capacities are necessary to more accurately assess population trends and responses. This study examines the relationships between track width, female body size (as measured by straight and curved carapace lengths and widths), and nesting variables (chamber depth, clutch size, and hatching success) of loggerhead turtles (*Caretta caretta)* nesting in southeastern Florida. Track width was significantly positively related to body size, and body size was significantly related to both chamber depth and clutch size. Only chamber depth showed a significant positive relationship with track width and could be predicted from track width measurements taken by a flexible measuring tape. Models such as these provide a low-cost tool that can allow for the analysis of sea turtle population changes over time in conjunction with environmental variation, as well as enable comparisons between past, present, and future nesting populations at much larger scales than currently possible.

Keywords: Sea turtle, nesting, loggerhead, track width, carapace length, carapace width, chamber depth

Introduction

Sea turtles inhabit coastal and oceanic ecosystems across the globe, most commonly in tropical, subtropical, and temperate climates. They facilitate many ecosystem services that promote the overall health and long term success of their core-use habitats, including increasing nutrient cycling and availability throughout neritic, pelagic, benthic, and beach environments (Heithaus 2014). Unfortunately, global turtle populations are widely impacted by climate change, which can affect their supply of food and resources, foraging habits, and alter reproductive processes. They also continuously suffer from increasing anthropogenic destruction of nesting and foraging habitats, fisheries bycatch, and increasing boat traffic (Bjorndal et al. 2013; Hart et al. 2014; Bjorndal et al. 2017). Of the seven extant sea turtle species, six of these inhabit the waters of the United States: loggerhead (*Caretta caretta*), green (*Chelonia mydas*), leatherback (*Dermochelys coriacea*), hawksbill (*Eretmochelys imbricata*), Kemp's ridley (*Lepidochelys kempii*), and olive ridley (*Lepidochelys olivacea*). All six species are federally protected in the United States through the Endangered Species Act of 1973 and are listed as either endangered: green (Seminoff 2004), hawksbill (Mortimer, Donnelly, and IUCN SSC Marine Turtle Specialist Group 2008), and Kemp's ridley (Wibbels and Bevan 2019); or vulnerable: loggerhead (Casale and Tucker 2017), leatherback (Wallace, Tiwari, and Girondot 2013), and olive ridley turtles (Abreu-Grobois, Plotkin, and IUCN SSC Marine Turtle Specialist Group 2008) (Ocean Studies Board and National Research Council 2010; Marine Turtle Specialist Group 2018).

The Atlantic coast of Florida is a critical nesting habitat for loggerhead turtles in the western hemisphere (Weishampel, Bagley, and Ehrhart 2004; Bovery 2014). Florida enforces state protections for this species and hosts approximately 90% of nesting for the North Atlantic loggerhead population, as well as 40% of total global loggerhead nesting (Florida Fish and Wildlife Conservation Commission 2016). Their imperiled status highlights the pressing importance of recording accurate demographic parameters (e.g., growth rates, fecundity) and abundance estimates to fill in gaps in the data records and create effective conservation strategies. Historically, these data have been difficult to obtain due to many life-history characteristics of sea turtles, such as long lifespans with delayed maturity and iteroparity, low hatchling survival rates, wide habitat ranges, and highly migratory behavior (Crouse, Crowder, and Caswell 1987; Van Buskirk and Crowder 1994; Heppell 1998; Miller 2002; Ocean Studies Board and National Research Council 2010; Avens et al. 2013; Bjorndal et al. 2013; Avens et al.

2015). These characteristics result in slow population growth rates; and while sea turtles are naturally vulnerable to a variety of environmental threats throughout their different life-stages, they are now also vulnerable to anthropogenic influences at every life-stage. These factors, combined with the challenge of accessing the species on a consistent basis, consequently contribute to delayed observation of how populations are responding to environmental changes (Frazer and Richardson 1985; Mazaris, Fiksen, and Matsinos 2005; Casale, Mazaris, and Freggi 2011; Bjorndal et al. 2017).

Due to the difficulty of studying real-time sea turtle abundances and demographics at large scales, which results from their life-history characteristics, models must be used to estimate population parameters (Frazer 1984; Crouse, Crowder, and Caswell 1987; Heppell 1998; Miller 2002; Mazaris, Fiksen, and Matsinos 2005; Snover, Avens, and Hohn 2007; LeBlanc et al. 2014; Fujisaki, Lamont, and Carthy 2018). Historically, models have been based overwhelmingly on data acquired from nesting females, which only make up about 1% of the overall population (Ocean Studies Board and National Research Council 2010). Although females emerging on the beach to nest are of greatest convenience for data collection, there is still a large proportion of the population that goes unrepresented in these models. A large data deficit exists for the majority of male and juvenile sea turtles, as well as for offshore behaviors of both males and females (Schroeder, Foley, and Bagley 2003; Goshe et al. 2010; Avens et al. 2015). Most current models are also limited by the highly variable age at maturation within and between species, which depends on the growth rates of individual turtles and the specific method used to determine age. There is also a lack of long-term time-series data to reference current population data back to, which make it challenging to assess true survival rates and population growth changes over time (Congdon and van Loben Sels 1993; Goshe et al. 2010; Ocean Studies Board and National Research Council 2010; Avens et al. 2013; Prieto-Torres and Hernández-Rangel 2015). Environmental factors, such as air and sea surface temperatures, storms, and beach erosion, affect parts of the nesting process, including nest abundances, the timing of nest deposition, clutch size, hatching success, foraging and migration patterns, and growth rates of different sea turtle species (Weishampel, Bagley, and Ehrhart 2004; Hart et al. 2014; Lamont and Fujisaki 2014). The high variability of environmental factors and their effects on population structure make it challenging to quantify and incorporate such elements into a model. Until it is more feasible to integrate this natural variability into population models, focus can be shifted towards recording the most accurate demographic parameters to use in predictive models to fill in current data gaps and best improve conservation strategies (Schroeder, Foley, and Bagley 2003; Ocean Studies Board and National Research Council 2010). This study will contribute to filling these data gaps by establishing relationships between turtles and how they nest that previously have not been investigated.

The use of body size as an indicator for different physiological and ecological characteristics amongst vertebrates and using morphological traits to model body size trends is an established approach in many species (Sauer and Slade 1987). For example, human foot dimensions can be used as an indicator of height and weight (Gordon and Buikstra 1992; Fawzy and Kamal 2010); wing length in some species of birds can be an estimate for overall body size (Hamilton 1961; Wiklund 1996); and snout length in Chinese alligators (*Alligator sinensis*) can predict body length (Wu et al. 2006). Additionally, organism size often correlates with different aspects of fecundity, not only in turtles, but also in many species of fish, like the Coho salmon (*Oncorhynchus kisutch*) (Bagenal 1978; Berghe and Gross 1984), snakes (Seigel and Fitch 1985), lizards (Tinkle and Ballinger 1972), gray seals (*Halichoerus grypus*) (Anderson and Fedak 1985), and baboons (Sauer and Slade 1987). Population models incorporating turtle size typically use measurements of straight carapace length (SCL) and curved carapace length (CCL) as the body size indicator (Avens et al. 2012; Eguchi et al. 2012; Avens and Snover 2014; Bjorndal et al. 2017; Le Gouvello, Nel, and Cloete 2020). Some models have attempted to use body size to estimate age, often times from the back-calculation of growth rates through the use of skeletochronology, which analyzes growth marks on bones (Crouse, Crowder, and Caswell 1987; Snover, Avens, and Hohn 2007; Goshe et al. 2010; Avens et al. 2012; Avens et al. 2015). However, this method still has many limitations, including typically being restricted to deceased turtles with unknown causes of death, which can be problematic because diseased or malnourished turtles may not be representative of normal growth in populations (Avens and Snover 2014). These types of models, in conjunction with total track counts, have previously been used to estimate overall reproductive efforts of nesting females (Ocean Studies Board and National Research Council 2010). Previous studies have found positive relationships between turtle body size and track width, but each study used different measurements for body size. Plummer (1977) related track widths of the freshwater smooth softshell turtle *Tryionyx muticus*, to plastron length; and Miller (2002) related track widths of southeast Florida loggerheads to SCL.

This study examines the relationships between sea turtle track width, female body size, and three nesting variables of loggerhead turtles nesting on southeast Florida beaches. Body size will be measured by straight and curved carapace lengths (SCL and CCL, respectively) and straight and curved carapace widths (SCW and CCW, respectively). Many previous studies have shown that female body size positively correlates with multiple nesting variables, including: chamber depth (Chen and Cheng 1995; LeBlanc et al. 2014), clutch size (Frazer and Richardson 1986; Bjorndal and Carr 1989; Hays and Speakman 1991; Miller 2002; Broderick et al. 2003; LeBlanc et al. 2014; Avens et al. 2015; Prieto-Torres and Hernández-Rangel 2015; Le Gouvello, Nel, and Cloete 2020), egg size (Bjorndal and Carr 1989; Van Buskirk and Crowder 1994; LeBlanc et al. 2014), foraging mode and fecundity (Hawkes et al. 2006), hatchling health (Chen and Cheng 1995), and overall reproductive effort (Van Buskirk and Crowder 1994). This study specifically examines chamber depth, clutch size, and hatching success of nests and how they relate to body size and track width. First, we examined how body size affects track width, and next examined how body size affects the three nesting variables. Finally, we investigated if track width is related to each of the nesting variables with the ultimate goal of creating models that can predict the nest variables and body size using only track width data of nesting female loggerheads.

Acquiring body size and nesting data from track width measurements is advantageous for many reasons. First, it is a low cost, non-invasive method that requires low effort from researchers and could lend itself to easy carapace length conversions (Miller 2002). Second, the technique is simple, which allows for large quantities of data to be amassed in relatively short amounts of time. These aspects combined could expand the benefits of the proposed predictive models to numerous conservation programs, especially if programs lack the resources to measure carapace lengths and gather extensive nesting data. Models that successfully predict turtle size and nesting variables can provide accurate estimates to fill in current data gaps. This could lead to the standardization of nesting data across various programs and geographical regions, eventually enabling comparisons between subpopulations and analysis of population trends at larger scales than was previously possible. Furthermore, a predictive model will allow for the analysis of population changes over time in conjunction with environmental variation, as well as enable comparisons between past, present, and future projected populations. The hypotheses for this study are: (1) Track width is positively related to female body size; (2) female body size is positively related to chamber depth, clutch size, and hatching success; and (3) track width is predictive of chamber depth, clutch size, and hatching success.

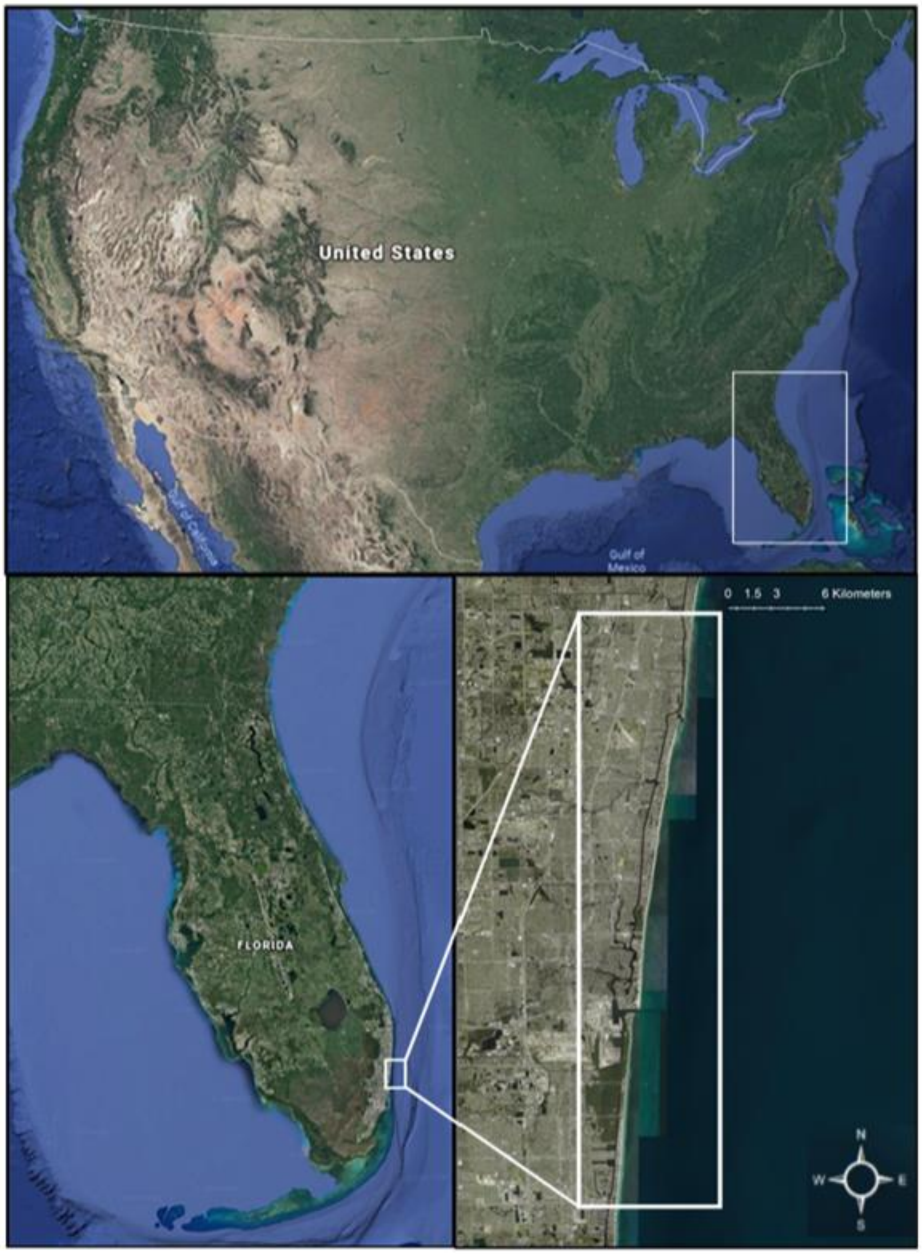

Figure 1. Location of the study area, Broward County, Florida.

Materials and Methods

Study Site

The study occurred in Broward County, which contains roughly 38 km of sandy beach nesting habitat and is located along the southeast Florida coastline, USA (Fig. 1). Broward County can host upwards of 3,000 or more sea turtle nests per season, 80-95% of which are laid by loggerheads (Burkholder and Slagle 2018). The specific survey zones included Hillsboro and Fort Lauderdale beaches, with Hillsboro having the highest nesting density in the county.

Data Collection

Nighttime beach surveys were conducted from early May to the end of August, the peak nesting period locally, in the years 2019 and 2020. Beaches were patrolled by a small crew of up to six surveyors between the hours of 9:00 pm and 5:00 am for female loggerheads that had completed nesting or were returning to the ocean after a "false crawl" (i.e., an unsuccessful nesting attempt). Individual turtles were detained on a flat portion of the beach within a portable four-sided corral, following methods similar to those in Hart et al. (2010). After being safely

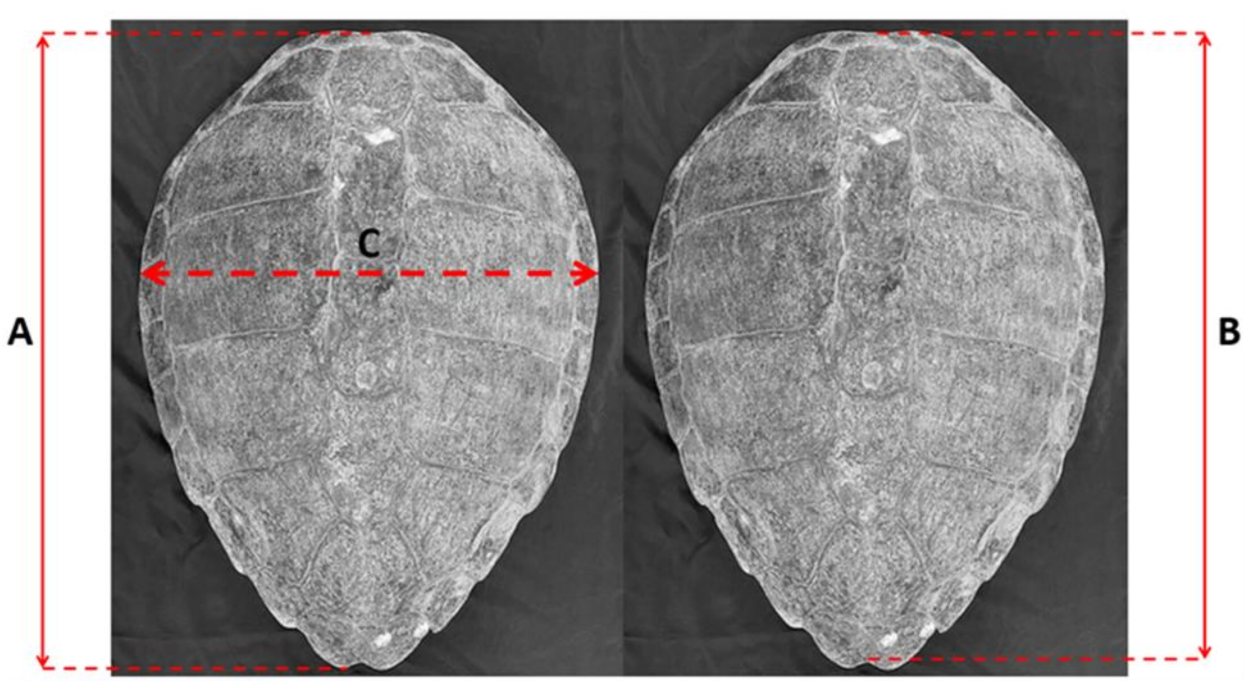

Figure 2. Photograph of loggerhead carapace illustrating how each body metric was measured. Each measurement is the same for both curved and straight measurements. (A) Straight and curved carapace length measured notch to tip (SCL tip and CCL tip). (B) Straight and curved carapace length measured notch to notch (SCL Notch and CCL Notch). (C) Straight and curved carapace width (SCW and CCW).

detained, turtles were measured and their carapace dimensions were recorded. Trained, permitted surveyors recorded straight carapace length from notch to notch (SCL notch), notch to tip (SCL tip), and straight carapace width (SCW) using straight-forked tree calipers. Curved carapace length was recorded from notch to notch (CCL notch), notch to tip (CCL tip), and curved carapace width (CCW) using flexible measuring tape. SCL and CCL from notch to notch was measured as the distance from the midline of the nuchal scute to the midline between the supracaudals. SCL and CCL from notch to tip was measured as the distance from the midline of the nuchal scute to the posterior tip of the supracaudals. Carapace width measurements were taken at the widest point of the carapace (Fig. 2).

Track width measurements were also taken at night for each turtle sampled. Loggerhead crawls are characterized by alternating comma-shaped rear flipper marks. Thus, track widths for loggerheads represent the minimum distance between indentations left by the claws of the rear flippers, taken as the distance from the bottom of one claw indent to the average distance between the opposite indents (Fig. 3). Tracks of each turtle were measured at two points along the incoming crawl, one point at or near the tide line where the sand was typically wet, and another point approximately midway to the nest laid or to the apex of the crawl if the turtle did not nest, where the sand was typically dry (weather permitting). Both points were measured with flexible measuring tape as well as with straight-forked tree calipers. This method produced four track width measurements per crawl for each surveyor that measured: (1) the high tide point measured with flexible tape (FHT), (2) the high tide point measured with calipers (CHT), (3) the midway point measured with flexible tape (FMD), and (4) the midway point measured with calipers (CMD). If crawls were measured by more than one surveyor, each of the four points were averaged with the measurements of the other surveyors to give only one FHT, FMD, CHT, and CMD measurement per turtle. Each crawl was measured by as many surveyors on the crew as possible, typically between two and four, to control for sampling error as well as accounting for natural variations in width along the crawl. All nighttime data collection was taken in collaboration with an ongoing research project of Dr. Derek Burkholder and Glenn Goodwin under the Florida Fish and Wildlife Conservation Commission Marine Turtle Permit #MTP-255.

The nesting variables (chamber depth, clutch size, and hatching success) were measured and recorded during morning survey nest inventories conducted by permitted researchers of the Broward County Sea Turtle Conservation Program (BCSTCP) under FWC Marine Turtle Permit

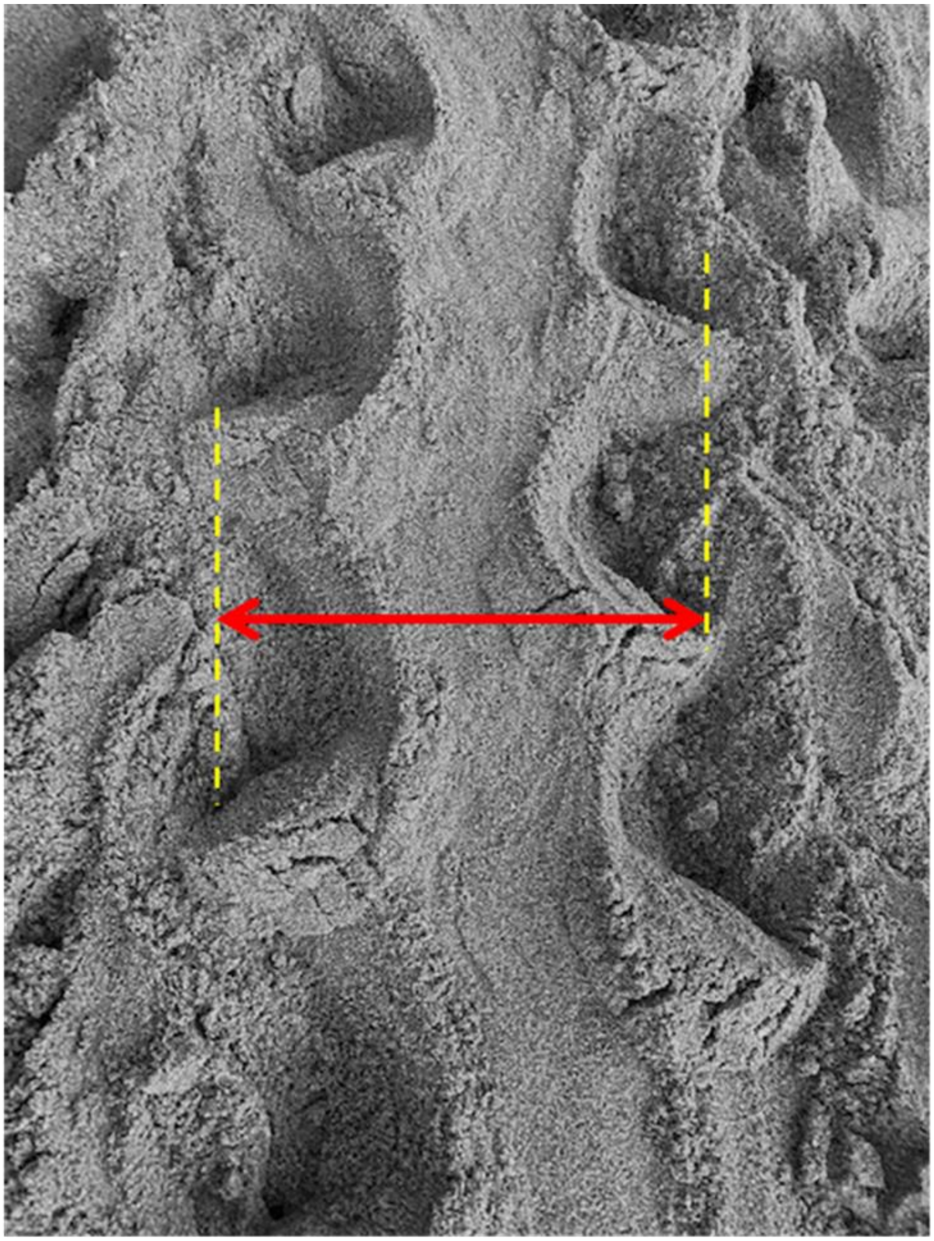

Figure 3. A loggerhead crawl. Track width is measured as the distance from the bottom of one claw indent to the average distance between the opposite indents, as indicated by the red arrow.

#MTP-214. Chamber depth is defined here as the distance from the bottom of the egg chamber to the level sand at the top of the nest; clutch size is the total number of eggs per nest; and hatching success is the percentage of eggs that hatched per nest. Nest inventories followed the protocol outlined in Burkholder and Slagle (2018) and the FWC Marine Turtle Conservation Handbook (Florida Fish and Wildlife Conservation Commission 2016). BCSTCP employees also took one measurement of track width for nest-associated crawls on their daily morning nesting surveys.

They used only flexible measuring tape, usually near the high tide line on the incoming track, following the same method illustrated in Figure 3. Chamber depth measurements that had noted sand accretion from heavy tides or storms, as well as track widths that noted rear flipper injuries, were excluded from all analysis.

Statistical Analysis

Paired T-tests were used to first determine if the four track width measurements taken at night were statistically different from each other. If there was no statistical difference between measurements taken with the flexible tape or calipers and no difference between measurements at the tide line or midway up the track, all four track measurements were averaged to give one track width measurement per turtle. Pearson's parametric correlations determined the covariance between each of the morphometric measurements and were used to decide which body size metric, or metrics, to test against track width. If body metrics showed high covariance ($r > 0.90$) with other body metrics of the same measuring method (i.e., curved or straight), then only one of those metrics would be selected for use in further analysis.

Ordinary Least Squares Regressions (OLS) were first used to determine if a relationship existed between average track widths and each of four body metrics (SCL tip, CCL tip, SCW, and CCW), with track width as the response variable. This model was used to predict track width values from carapace measurements taken in 2018, and a paired T-test determined if there was a

Table 1. Summary data of the loggerhead track widths and morphometric parameters measured in this study. All measurements taken in centimeters.

Parameter	Mean ± SD (n)	Minimum	Maximum
Track Width	50.1 ± 5.90 (79)	38.5	68
SCL Tip	88.6 ± 5.13 (79)	78.7	99.8
SCL Notch	87.6 ± 5.26 (79)	77	98.6
SCW	67.8 ± 4.97 (78)	54.9	76.8
CCL Tip	95.3 ± 5.92 (79)	77.4	107.5
CCL Notch	94.4 ± 5.89 (79)	75.6	106.9
CCW	88.2 ± 5.62 (77)	78.5	102

SCL Notch= straight carapace length measured notch to notch; SCL Tip= straight carapace length, measured notch to tip; SCW= straight carapace width; CCL Notch= curved carapace length, measure notch to notch; CCL Tip= curved carapace length, measured notch to tip; CCW= curved carapace width. For each parameter, the mean ± standard deviation (SD), sample size (n), and minimum and maximum values are shown.

significant difference between the predicted values and the actual track widths of those turtles taken by BCSTCP.

Next, Pearson's correlations and OLS were used to investigate relationships between the morphometric measurements and each of the nesting variables: chamber depth, clutch size, and hatching success. Once a significant relationship between a body metric and nest variable was identified, OLS was again used to explore predictive relationships between the significant nesting variables and track width, this time with track width as the predictor and nest variable as the response. When a nest variable showed a significant relationship with track width, the model was used to predict nest variable measurements for each nest from the 2018 BCSTCP track width measurements of the corresponding turtles. A paired T-test determined if there were significant differences between the predicted values for each nest and the actual values measured in 2018. All data were tested for normality with Shapiro-Wilk and linearity by examining the Residuals vs. Fitted values plot. All variables were normally distributed and linear except for hatching success, which was transformed using the arcsine transformation to achieve normality. Statistical analyses were conducted using RStudio, version 3.6.3 and statistical significance was determined by $p \leq 0.05$.

Table 2. Results of the correlations between each body size measurement to illustrate covariance among similar metrics. Straight measurements were taken with straight-forked tree calipers. Curved measurements were taken with flexible measuring tape.

Morphometrics Correlated	Correlation Coefficient (r)	P-Value
SCLN ~ SCLT	0.978	< 0.001
SCLN ~ SCW	0.730	< 0.001
SCLT ~ SCW	0.690	< 0.001
CCLN ~ CCLT	0.984	< 0.001
CCLN ~ CCW	0.816	< 0.001
CCLT ~ CCW	0.822	< 0.001
SCLN ~ CCLN	0.920	< 0.001
SCLT ~ CCLT	0.897	< 0.001
SCW ~ CCW	0.802	< 0.001

SCLN= straight carapace length, measured notch to notch; SCLT= straight carapace length, measured notch to tip; SCW= straight carapace width; CCLN= curved carapace length, measure notch to notch; CCLT= curved carapace length, measured notch to tip; CCW= curved carapace width.

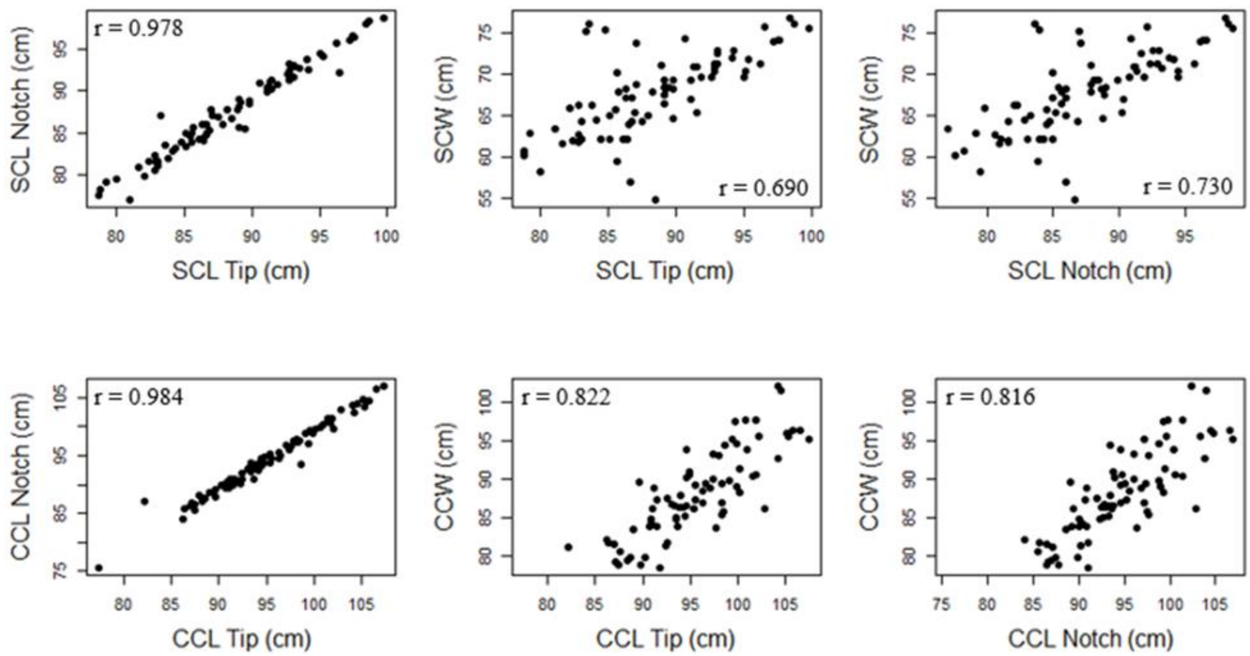

Figure 4. Correlations between body size metrics. SCL Notch= straight carapace length measured notch to notch; SCL Tip= straight carapace length, measured notch to tip; SCW= straight carapace width; CCL Notch= curved carapace length, measure notch to notch; CCL Tip= curved carapace length, measured notch to tip; CCW= curved carapace width. See Table 2 for each correlation coefficient and p-value.

Results

Track width and carapace measurements were taken for 44 loggerhead turtles in 2019 and 35 loggerheads in 2020 (n = 79; Table 1). The four track width measurements taken at night along each crawl were not significantly different from each other, so track widths for each turtle were consistent regardless of the measuring tool used and the point along the crawl. The four measurements (FHT, FMD, CHT, and CMD) were then averaged for each turtle to produce only one average track width measurement per turtle for simplification of the models going forward. The morning track width measurements taken by BCSTCP were also not significantly different from the nighttime track width averages taken for the same turtles, so measuring methods were followed consistently across all surveyors and comparisons could be made across nighttime and daytime track width measurements.

The morphometric data showed high covariance among both straight and curved measurements (Fig. 4). When SCL and CCL notch and SCL and CCL tip measurements were correlated with SCW and CCW measurements, respectively, all correlations were positive and significant but had coefficients below 0.90 (Table 2). There were very strong positive correlations between SCL tip and SCL notch (r = 0.978, p = < 0.001), and CCL tip and CCL notch (r = 0.984, p = < 0.001). Therefore, in order to reduce redundancy in the models, only SCL tip, CCL tip, SCW, and CCW measurements were chosen to test for relationships with average track widths while SCL notch and CCL notch were excluded from further analysis due to their strong covariance with SCL tip and CCL tip. Some carapaces lacked distinct posterior notches due to natural variation in carapace shape, therefore measurements to tip were more consistent.

The relationships between track width and body size varied slightly with the morphometric parameter used, but the overall trend showed that larger loggerhead females had larger track widths (Fig. 5). The linear relationship between CCL tip and track width ($F_{1,76}$ = 10.47, R^2 = 0.121, p = 0.0018) was stronger than the linear relationship between SCL tip and track width ($F_{1,76}$ = 3.85, R^2 = 0.048, p = 0.0534), with the latter showing only marginal significance. Both models predicted track width without a significant difference (p_{SCL} = 0.3079, p_{CCL} = 0.2116) from the actual track width measurements recorded in 2018 by BCSTCP on their

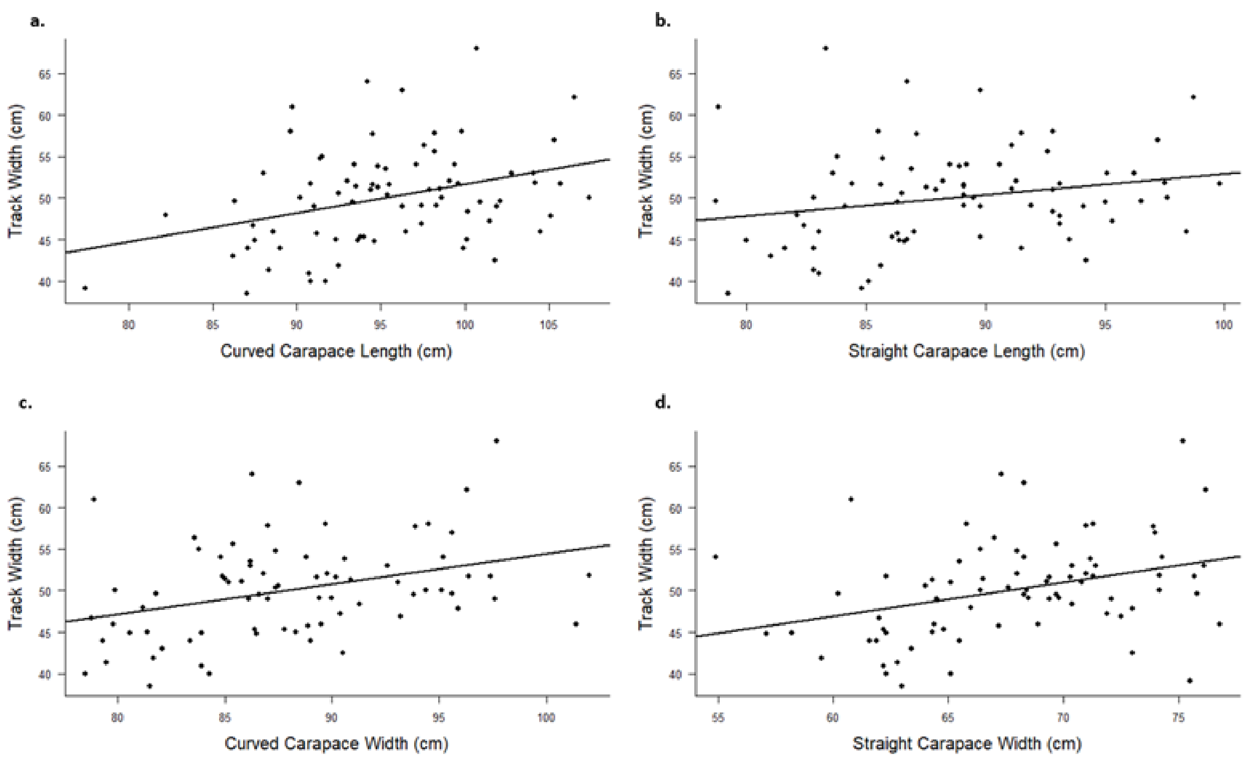

Figure 5. Relationships between loggerhead (a) curved carapace length and track width (y = 17.0081 + 0.3467x, R^2 = 0.121), (b) straight carapace length and track width (y = 27.6497 + 0.2529x, R^2 = 0.048), (c) curved carapace width and track width (y = 18.1158 + 0.3634x, R^2 = 0.123), and (d) straight carapace width and track width (y = 22.2097 + 0.4116x, R^2 = 0.1198).

morning surveys. The linear relationship between SCW and track width ($F_{1,75} = 10.21$, $R^2 = 0.120$, $p = 0.002$) was about as strong as that of CCW and track width ($F_{1,74} = 10.35$, $R^2 = 0.123$, $p = 0.0019$). Both models were again able to predict track width without significant difference ($p_{SCW} = 0.3943$, $p_{CCW} = 0.3195$) from the actual 2018 measurements.

Not all turtles that were measured for body size nested, and not all confirmed nests hatched or were able to be inventoried. This limited the sample size used to create the models incorporating the nesting variables compared to the models using only track width and carapace measurements. Chamber depth, clutch size, and hatching success were obtained from 15 loggerhead nests in 2019 and 19 loggerhead nests in 2020 (n = 34; Table 3). Each of the four body size metrics individually had a significant effect on chamber depth, showing that overall larger turtles dig deeper egg chambers (Fig. 6). Ordinary Least Squares regression models using SCW ($F_{1,32} = 13.4$, $R^2 = 0.295$, $p = 0.0009$) and CCW ($F_{1,31} = 21.8$, $R^2 = 0.413$, $p < 0.001$) showed slightly stronger linear relationships with chamber depth compared to the models using SCL tip ($F_{1,32} = 8.58$, $R^2 = 0.211$, $p = 0.0062$) and CCL tip ($F_{1,32} = 12.3$, $R^2 = 0.278$, $p = 0.0014$) measurements. The relationship between CCW and nest chamber depth provided the best model (Fig. 6g), where CCW explains approximately 41% of the variability in chamber depth.

Clutch size was also significantly affected by each of the four body size metrics individually. This time, the models using SCL tip ($F_{1,34} = 38.3$, $R^2 = 0.530$, $p < 0.001$) and CCL tip ($F_{1,34} = 73.4$, $R^2 = 0.684$, $p < 0.001$) showed slightly stronger linear relationships with clutch size and explained a greater percent of the variability than the models using SCW ($F_{1,34} = 10.8$,

Table 3. Summary data of the loggerhead track widths and nesting variables measured in this study.

Parameter	Mean ± SD (n)	Minimum	Maximum
Track Width (cm)	50.1 ± 5.90 (79)	38.5	68
Chamber Depth (cm)	54.7 ± 7.59 (34)	41	68
Clutch Size (number of eggs)	100.7 ± 23.3 (34)	56	153
Hatching Success (%)	82.1 ± 21.6 (34)	0	100

Chamber depth is measured as the distance from the bottom of the egg chamber to the level sand at the top of the nest. Clutch size is the total number of eggs per nest. Hatching success is the percentage of eggs that hatched in each nest. For each parameter, the mean ± standard deviation (SD), sample size (n), and minimum and maximum values are shown.

$R^2 = 0.240$, $p = 0.0024$) and CCW ($F_{1,33} = 23.8$, $R^2 = 0.419$, $p < 0.001$). The relationship between CCL tip and clutch size provided the best model, with approximately 68% of the variability in clutch size explained by the CCL of the nesting female. Contrary to these findings, the hatching success rates of loggerhead nests were not significantly related to any of the body size metrics ($p >> 0.05$) and were not correlated to chamber depth or clutch size.

Track width was significantly related to all four body size metrics (Fig. 5), and those morphometrics were all significantly related to both chamber depth and clutch size of loggerhead nests (Fig. 6). Additionally, chamber depth and clutch size were significantly correlated (r =

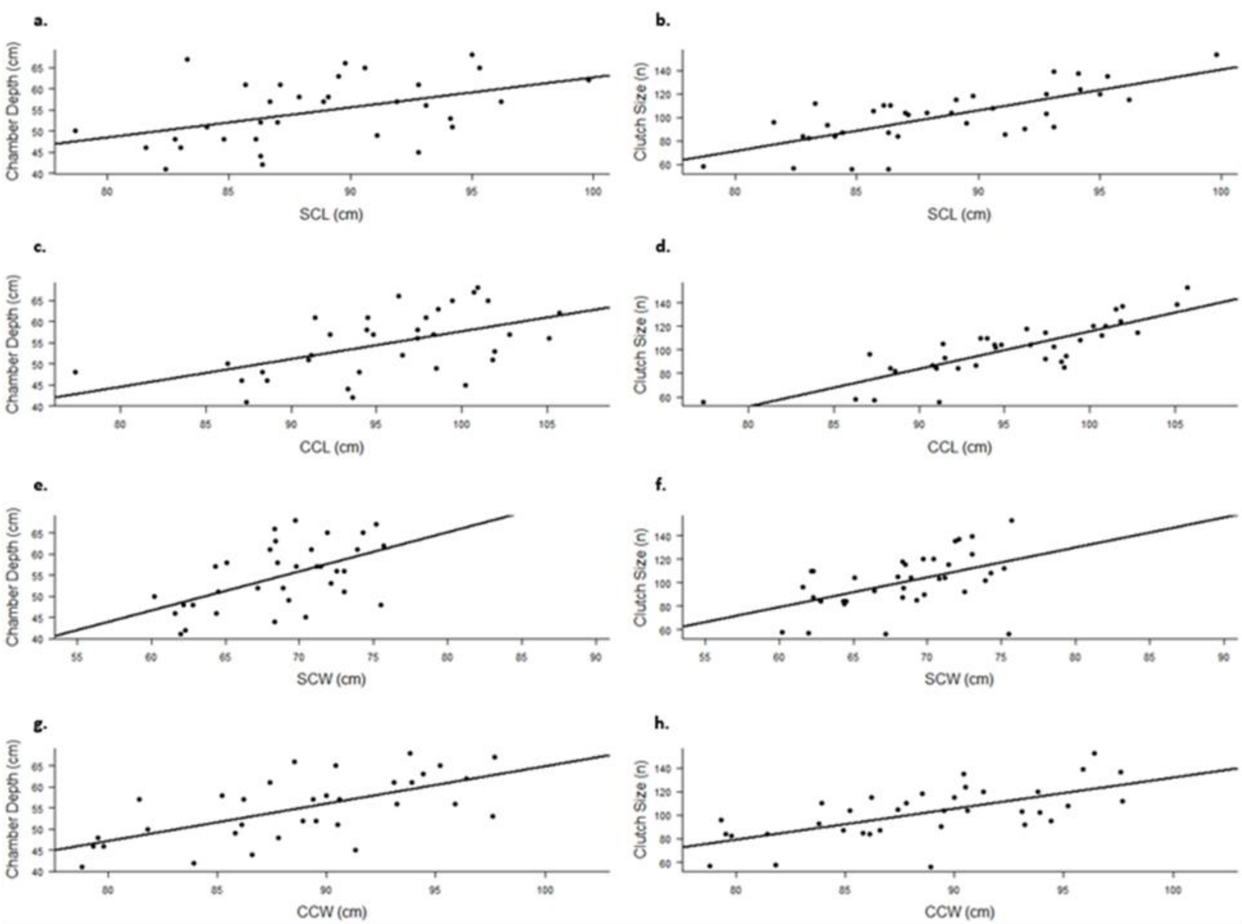

Figure 6. Relationships between loggerhead (a) straight carapace length (SCL) and nest chamber depth ($y = -8.8672 + 0.7166x$, $p = 0.0062$); (b) SCL and clutch size ($y = -208.4447 + 3.4931x$, $p < 0.001$); (c) curved carapace length (CCL) and chamber depth ($y = -7.8763 + 0.6557x$, $p = 0.0014$); (d) CCL and clutch size ($y = -204.2591 + 3.2015x$, $p < 0.001$); (e) straight carapace width (SCW) and chamber depth ($y = -9.0824 + 0.9286x$, $p < 0.001$); (f) SCW and clutch size ($y = -74.6916 + 2.5606x$, $p = 0.0024$); (g) curved carapace width (CCW) and chamber depth ($y = -23.7521 + 0.8863x$, $p < 0.001$); (h) CCW and clutch size ($y = -132.4353 + 2.6474x$, $p < 0.001$).

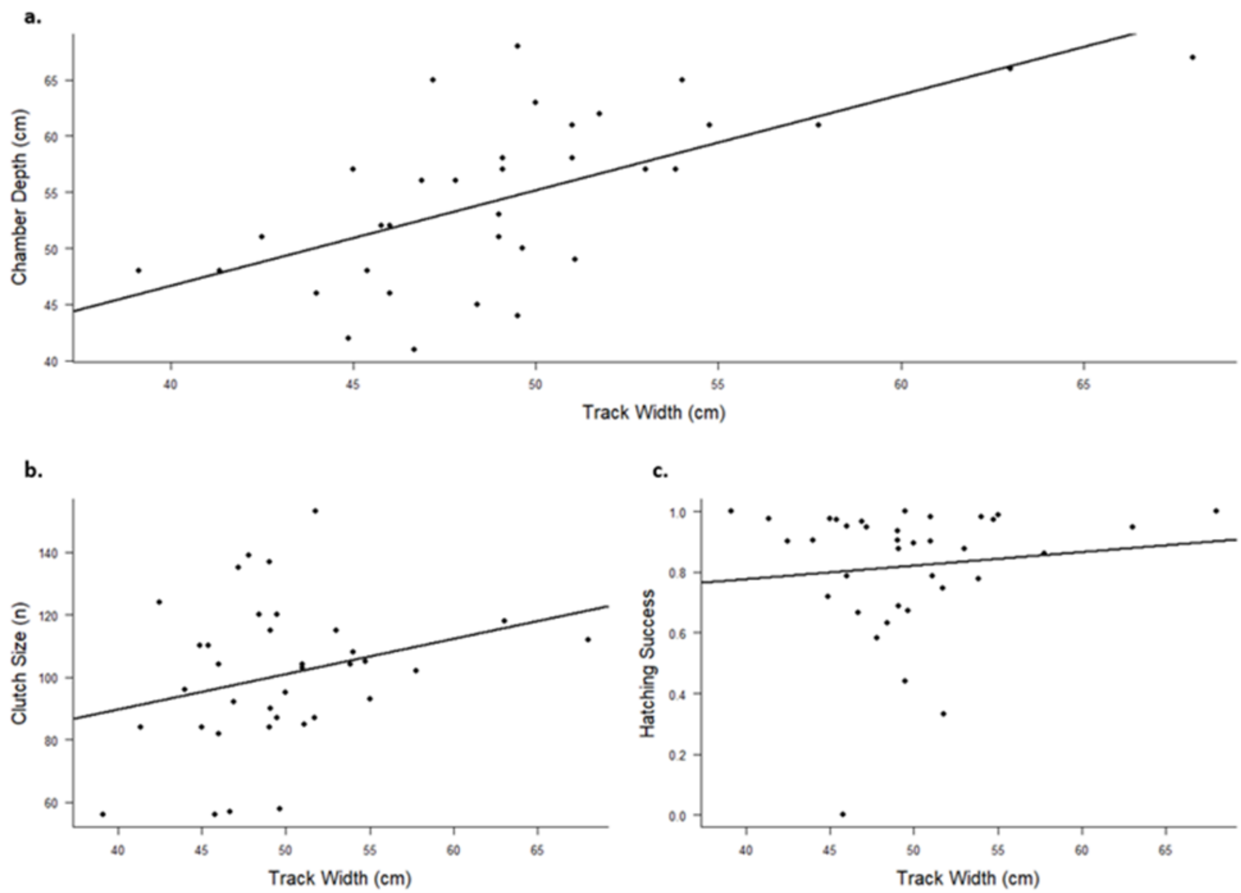

Figure 7. Relationships between loggerhead track width and (a) nest chamber depth ($y = 12.7686 + 0.8489x$, $R^2 = 0.402$, $p < 0.001$), (b) clutch size ($p = 0.108$), and (c) hatch success ($p = 0.424$).

0.468, $p = 0.0053$). Therefore, it was expected that both nest variables would also relate to track width. Track width significantly affected chamber depth ($F_{1,32} = 21.5$, $R^2 = 0.402$, $p < 0.001$) and explained approximately 40% of the variability in chamber depth (Fig. 7a). The model successfully predicted chamber depth values without significant difference ($p = 0.144$) from the actual 2018 measurements collected by BCSTCP. However, track width was not related to clutch size ($p = 0.108$) and could not be used to predict accurate clutch sizes (Fig. 7b).

Discussion

This study is the first to show that a significant relationship exists between nest chamber depth and female track width, and that this specific model can predict chamber depth with no significant difference from the actual chamber depths solely from track width measurements using only a flexible measuring tape. This result could be related to the ability of longer rear flippers to reach further depths in the ground and allow for deeper nests to be excavated. Nest

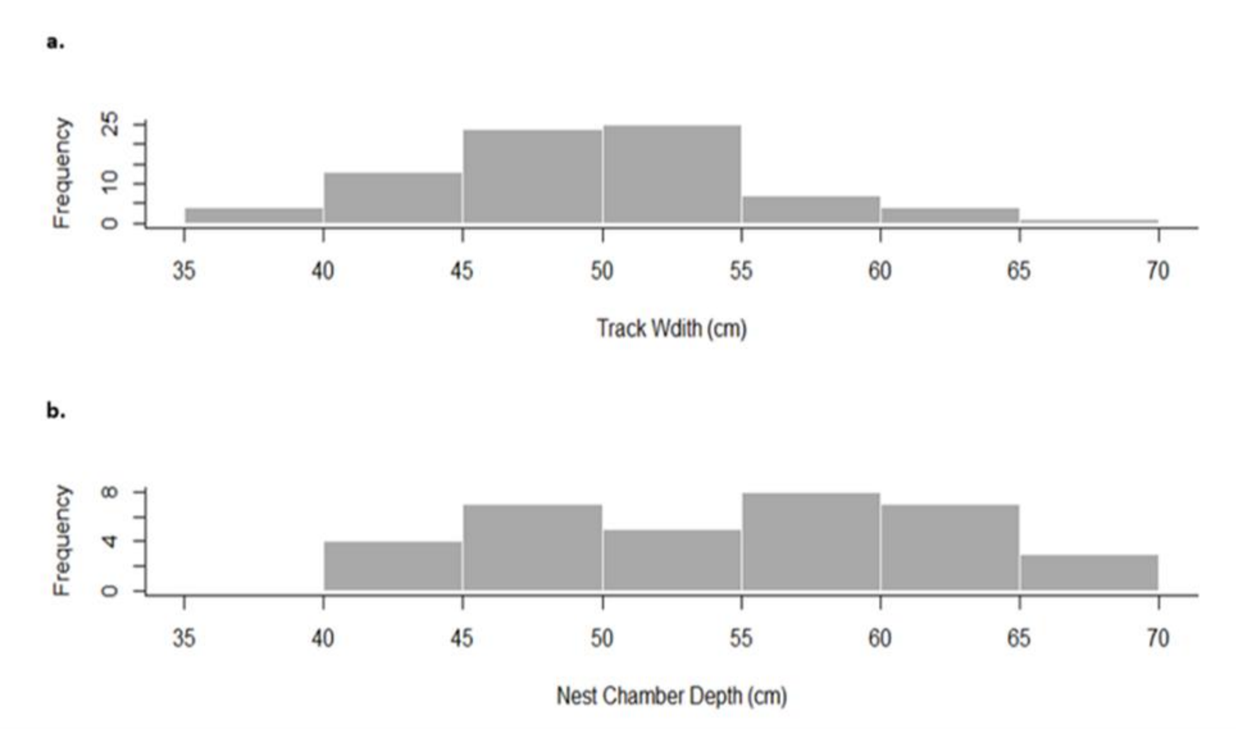

Figure 8. Frequency distribution of (a) track width measurements, ranging from 38.5-68 cm, and (b) nest chamber depths, ranging from 41-68 cm, of loggerhead females nesting in Broward County.

depths measured in this study ranged from 41 cm to 68 cm, and this range was nearly mirrored by the range of loggerhead track widths recorded, which was from 38.5 cm to 68 cm (Figure 8; Table 1). This finding further promotes the use of track width as a useful indicator of chamber depth. Even though track width was not significantly related to clutch size in this study, clutch size did show a significant positive correlation with nest depth and significantly related to all measurements of body size. This indicates that larger turtles dig deeper nests and lay larger clutches, which supports the findings of a multitude of past studies (Frazer and Richardson 1985; Bjorndal and Carr 1989; Hays and Speakman 1991; Miller 2002; LeBlanc et al. 2014; Avens et al. 2015; Prieto-Torres and Hernández-Rangel 2015; Le Gouvello, Nel, and Cloete 2020). Therefore, predicted chamber depths may still indirectly provide insight to approximate clutch size estimates.

Hatching success rates showed no relationship or correlation to any body size metric or other nest variable. This lack of association is not entirely surprising, probably because local environmental factors and the incubation environment play a larger role in successful embryonic development than any maternal characteristics (Foley, Peck, and Harman 2006; Erb, Lolavar, and Wyneken 2018). Nests near the high tide line are at risk of excessive washing over by the tide, or even total washout by heavy tides which results in total loss of the nest. Nests in open sand with no shading nearby may be exposed to too much solar heating, reaching internal temperatures that exceed the optimal range for healthy embryo development (Erb, Lolavar, and Wyneken 2018). Root presence from surrounding vegetation, shade, heavy storms, and predation are all factors that affect, and further complicate the prediction of the hatching success rates of a nest.

This study is also one of the first to demonstrate a significant positive relationship between track width and female body size, and the first to illustrate the relationship exists with three different body size metrics (CCL, SCW and CCW), not just one length measurement. Additionally, models were created that allow for prediction of track width from body size measurements without significant difference from the actual track widths, and these equations can be rearranged to predict the body size from track width as well. However, it is important to note that even the strongest body size relationships, which were between track width and CCL, CCW, and SCW, only explained about 12% of the variability in track width. Therefore, despite the presence of the significant relationship, track width alone may not be the most accurate predictor of body size. Nevertheless the assumption that bigger turtles make wider tracks in the sand has been verified by very few studies and the application of predictive models founded on this could have major implications for the future of sea turtle conservation (Plummer 1977; Miller 2002). Such models have the potential to assess population demographics of nesting females without ever having to encounter them directly, which provides a new technique for analyzing nesting trends that is low cost, non-invasive, and lower effort compared to the approaches currently utilized.

The physical size of sea turtles is known to be strongly related to fecundity, informing the basis of many modern population models (Crouse, Crowder, and Caswell 1987; Hawkes et al. 2006; Avens et al. 2015). Fecundity encompasses the many aspects of maximizing reproductive output, and many of those aspects can be measured through beach surveys and post-hatch nest inventories, i.e., nest chamber depth. Analyzing a simple parameter such as this can offer insights to reproductive output that may not be immediately obvious (Marco et al. 2018). Chamber depth influences incubation temperatures, which directly affect sex determination of hatchlings (Chen and Cheng 1995; Avens et al. 2012; Wyneken, Lohmann, and Musick 2014).

Deeper nests typically have cooler incubation temperatures than shallower nests locally, and cooler incubation temperatures will favor a greater proportion of males hatched than females (Van De Merwe, Ibrahim, and Whittier 2006). By evaluating predicted chamber depth trends, it may be possible to inform some models on the productivity of future generations by contributing to ratio estimation of males to females that enter the population each year. However, this capability may be limited to regions with higher variability of local climates, because in places with consistently high air temperatures, such as south Florida, the differences in chamber depths may not be large enough to have a substantial impact on the sex of the hatchlings.

Digging deeper nests could appear to be a drawback for the female and hatchlings because it requires greater energy expenditure from the females during the nesting process, increases time exposed to predators while digging, and forces greater effort from hatchlings while escaping the nest. But it has been shown that hatchling health is positively affected by maternal body size and that hatchlings from deeper nests exhibited quicker mobility responses, meaning they took significantly less time to right themselves when flipped on their backs, than the same number of hatchlings emerging from shallower nests (Chen and Cheng 1995; Marco et al. 2018). Thus, greater chamber depths dug by larger turtles may be indicative of nests that produce hatchlings with higher fitness levels and possess an early survival advantage. Overall, the ability to predict nest chamber depth from an indicator of body size could help improve the accuracy of population models and predictions of future population trends.

Nevertheless, the relationship between chamber depth and body size is still equivocal. Marco et al. (2018) found no relationship between this nesting variable and female body length, also noting that nest depth for each individual female was inconsistent. This could be due to a possible seasonal variation in chamber depths of individuals, or perhaps the existence of an optimum depth range for nests that females dig to regardless of body size. The study also speculated that warming global temperatures from climate change could act as a possible buffer for any temperature effects that deeper nests could have on hatchling sex ratios. Marco et al. (2018) also proposed the idea that digging deeper nests could be a way for sea turtles to maintain historical hatchling sex ratios irrespective of their physical size. Despite the significant relationships found in the current study, relatively low R^2 values were reported and likely due to high environmental variability and unaccounted external factors. The track width measurement is directly related to the turtle itself and any possible injuries it may have, as well as being influenced by the substrate type, sand compaction, beach slope, weather, and foot traffic on the beach, which could all distort the track in different ways. For these reasons, it is necessary to control for consistency in track width measurements as much as possible to allow for meaningful comparisons.

It is interesting that body size seemed to explain the most variability in, and relate most strongly to clutch size out of all the nesting variables tested, yet clutch size did not relate to track width. While larger females maximize their reproductive efforts by laying more eggs per clutch instead of more total clutches, loggerhead clutch sizes often tend to decrease throughout the nesting season as maternal resources are depleted, regardless of body size (Bjorndal and Carr 1989; Congdon and van Loben Sels 1993; Broderick et al. 2003; LeBlanc et al. 2014). If deeper nests are dug to hold larger clutches, then it is possible that chamber depth could decrease steadily as clutch size decreases. Thus, it's possible that larger turtles will still lay larger clutches in deeper nests than smaller turtles at similar points of resource depletion, which simultaneously maintains the body size gradient across nesting females and respective chamber depths. Clutch size ranges can be much more variable than chamber depth ranges, so track width measurements may not accurately reflect this seasonal progression towards smaller clutches, and there are still many unknowns about how resource depletion varies among individuals. Therefore, track width cannot be considered an accurate predictor of clutch size.

There are still many uncertainties pertaining to sea turtle reproduction and population demographics. While one subpopulation may exhibit a particular trend, another subpopulation may not. It is known that loggerhead size significantly varies between geographical regions, for example: loggerheads of the western north Atlantic have similar size ranges at maturity (based on straight carapace length), but are significantly different than the size ranges of mature loggerheads in the Mediterranean (Stoneburner 1980; Tiwari and Bjorndal 2000). This suggests that variations in environmental conditions lead to different morphological responses, and subpopulations are shaped by the stressors and resources specific to their habitat (Lamont and Fujisaki 2014; Fujisaki, Lamont, and Carthy 2018). For this reason, track width to body size relationships must be investigated on a region-by-region basis to create useful population-specific models, and it cannot be assumed that one model will fit all individuals of a species.

Further progress could be made by evaluating the presence of these trends in other subpopulations of loggerheads, such as in the Mediterranean, to determine if similar models can be applied to different populations. These relationships can also be investigated in other locally nesting species, i.e., green turtles in Broward County; and by looking for relationships with other nesting variables, or incorporating specific interactions of environmental variability. Future studies could also explore chamber depth or clutch size variation in subsequent nests of individuals throughout the season using mixed effect models with individual turtles as the grouping factor. Going forward, it is crucial to standardize methods of track width measurement for each species to expand the benefits of models based on track widths and enable model comparisons among different geographical regions.

Conclusion

The relationships established between track width and body size as well as between track width and chamber depth have numerous implications for conservation programs around the globe. They can increase the availability of crucial demographic and nesting trend data both locally and internationally. Generating models that can accurately predict specific aspects of fecundity from easily accessible track width data creates a valuable new technique for analyzing nesting trends. These models could entice programs to standardize the collection of nesting data to allow for larger scale analysis of sea turtle populations and how they change over time. Models will always have limitations, especially when working within the natural environment, but the impact potential of such low-cost and effective analysis tools are extensive and should not be overlooked. Although it may be difficult to tease apart the influences of maternally controlled factors and environmental factors, understanding any aspects that contribute to hatchling survival and provide early life advantages is crucial to finding the most effective conservation strategies (Van Buskirk and Crowder 1994; Marco et al. 2018; Le Gouvello, Nel, and Cloete 2020). It also aids in providing the most accurate predictions of population changes, which all together are essential to ensuring the survival of sea turtles in the modern world.

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