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Monograph

High variability in nest site selection in a loggerhead turtle rookery, in Boa Vista Island, Cabo Verde

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ABSTRACT

Among sea turtles, nest site selection is a crucial factor for hatching success and population viability. The relocation of otherwise doomed clutches to safe hatcheries has been widely promoted as a conservation strategy, although this may promote artificial selection of poorly adapted genotypes. In this study, we used multiyear spatial nesting data of individual loggerhead turtles (*Caretta caretta*) from one of the largest Atlantic rookeries, in Cabo Verde, across six consecutive nesting seasons (2013–2018), to identify spatial nesting patterns, assess how individual nest site selection is influenced by female size and age, and estimate the impacts on the reproductive output. Although females nested across the entire beach width, they preferentially nested in the middle of the beach, avoiding to nest both close to the tideline and close to the vegetation line. Hatching success decreased towards the waterline, while the risk of nest inundation or predation was high, regardless of nest location. In general, females showed high variability in nest site selection, except larger females (> 93 cm curved carapace length) that showed higher repeatability ($r = 0.50$, SE $= 0.14$, 95% CI: 0.16–0.72) in distances to the vegetation. We therefore suggest that the relocation of doomed clutches should be considered for this endangered rookery, as clutch relocation should not substantially distort the gene pool, assuming nest choice is a heritable trait. In addition, we recommend the preservation of beach vegetation, particularly in areas with human development.

1. Introduction

Sea turtles spend most of their lives in the marine environment, only coming ashore for brief periods to lay eggs. As they display no parental care, nest site selection in females is a crucial factor for offspring survival (Reising et al., 2015; Patrício et al., 2018). Nesting close to the tide line may expose the clutches to frequent flooding (Wood and Bjorndal, 2000; Kamel and Mrosovsky, 2004; Martins et al., 2022), whilst hatchlings that emerge from nests located further from the sea are at higher risk of suffering disorientation, dehydration and higher predation by land predators (Wood and Bjorndal, 2000; Martins et al., 2021a). Similarly, nest site selection may have implications for nesting female survival (Marco et al., 2012a, 2017). Females that nest farther inland spend more time exposed to terrestrial predators and may be more likely to become disoriented, trapped, and unable to return to the sea (Marco et al., 2017).

All species of sea turtle exhibit a similar nesting process, although there is marked variability in nest site selection between species, populations and even among individuals from the same population. In the green turtle (*Chelonia mydas*) rookery in Guinea Bissau for example, differences in nest site selection exist between groups of individuals, with some females preferring to nest closer to the vegetation and others demonstrating a preference for high beach elevation or forested areas (Patrício et al., 2018). Similarly, intra-population variability in nest site selection has also been observed in a nesting population of hawksbill sea turtles (*Eretmochelys imbricata*) in Guadeloupe, between females preferring to nest in littoral forest and places with overstory vegetation cover, and others preferring more open, deforested areas (Kamel and Mrosovsky, 2006). On the other hand, nesting populations of loggerhead turtles (*Caretta caretta*) in Australia (Pfaller et al., 2009; Kelly et al.,

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2017) and leatherback turtles (*Dermochelys coriacea*) in Playa Grande, Costa Rica (Nordmoe et al., 2004) showed no such variation in individual preferences for nesting site.

This individual variation in nesting site selection can have significant implications for the ecology, evolution and conservation of sea turtles (Kamel and Mrosovsky, 2004, 2006; Liles et al., 2015; Patrício et al., 2018). Cooler nests produce hatchlings that are larger, disperse faster and are more efficient in escaping predators (Martins et al., 2020), whilst warmer nests produce smaller hatchlings and female-biased hatchling sex ratios (Patrício et al., 2017; Martins et al., 2020). Variability in nest-site selection strategies is key from an evolutionary perspective, as individuals that exhibit high plasticity, or weak fidelity to particular beaches, are more likely to explore new nesting beaches. This can have multiple benefits, such as reducing density-dependent nest destruction (Girondot et al., 2002) and promoting the colonization of novel suitable environments (Kamel and Mrosovsky, 2004). Additionally, intrapopulation variability may enhance resistance to environmental disturbance and increase the adaptive response to changes in the environment (Snell-Rood, 2013; Patrício et al., 2018), with populations that display a wider range of thermal incubation conditions potentially exhibiting higher resilience to climate change (Abella et al., 2016; Patrício et al., 2019; Reid et al., 2019). Individual specialization may require biodiversity managers to use caution when generalizing conservation practices using data from the same or related species from different geographic locations (Mrosovsky, 2006; Pfaller et al., 2009; Liles et al., 2015). Knowledge of individual patterns of nest site selection among sea turtles is thus essential to improve the planning of conservation activities and further our understanding of how sea turtles might fare under future climatic conditions.

Research interest in sea turtle nest site selection and its potential responses to environmental change has increased recently (Kamel and Mrosovsky, 2004, 2006; Pfaller et al., 2009; Liles et al., 2015; Hatase and Omuta, 2018; Patrício et al., 2018). The topic is now considered a research priority for sea turtle management and conservation (Rees et al., 2016). There are still, however, major geographic information gaps, and some key populations remain understudied. This is the case for the nesting loggerhead population in Cabo Verde, considered a distinct Eastern Atlantic Regional Management Unit (RMU) (Wallace et al., 2010). This RMU is classified as “Endangered” by the IUCN (Casale and Marco, 2015). In this rookery, females nest primarily on small beaches across the archipelago (Marco et al., 2012a; Ferreira-Veiga, 2018; Laloë et al., 2019), with >85% of nesting activity occurring on beaches with a low elevation profile, vulnerable to spring-tides (Ferreira-Veiga, 2018), and with a high presence of tourists (Marco et al., 2011; Laloë et al., 2019). Clutches experience high mortality due to both natural and anthropogenic impacts, namely tidal inundation, high levels of predation by ghost crabs (*Ocypode cursor*), sand removal, pollution, and tourism-associated coastal development (Sarmiento-Ramírez et al., 2010; Marco et al., 2011, 2015, 2018, 2021; Martins et al., 2021b).

Here, we provide information on spatial nesting patterns and explore how nest site selection may affect offspring survival in the loggerhead population from Cabo Verde. We use global positioning system (GPS) data and Geographic Information Systems (GIS) to identify patterns of nest placement by female loggerhead turtles within (from June to October) and between (from 2013 to 2018) nesting seasons. In addition, we assess if loggerhead turtles show preferences for specific nesting sites (e.g. closer to the vegetation or to the tide line), and investigate the influence of female size and age on nest site selection. Lastly, we investigate the relationship between nest placement and hatching and emergence success.

2. Methods

2.1. Study site

This study was carried out on João Barrosa beach, a 5 km long beach on the south-eastern coast of Boa Vista Island in the Cabo Verde Archipelago off West Africa (Fig. 1). João Barrosa is a relatively flat beach with a small dune system up to 2 m above sea level, covered by small herbaceous scrub of *Zygophyllum* spp. and *Arthrocnemum glaucum* (Silva et al., 2017). A designated Ramsar wetland site exists behind the beach (Curral Velho, Site code number: 1575). The shoreline is clear of obstacles (rocks or reefs) and the beach is within the Sea Turtle Natural Reserve (STNR; Decree law No. 14/2013). It represents one of the most important nesting areas for the loggerhead turtle in Cabo Verde, with an average of 3987 clutches laid annually, corresponding to approximately 800 nesting females in each nesting season (Marco et al., 2012a, 2018; Martins et al., 2021b). Human presence in the area is very low, with no human settlement except the temporary sea turtle field camp constructed annually during the nesting season (from June until October). The research was approved by the National Directory of the Environment of Cabo Verde and received ethical approval following strict international animal care guidelines (permit numbers: DGA, 21/2013; 22/2015; DNA, 16/2016; 51/2018).

2.2. Data collection

Beach monitoring was conducted from 20:00 to 07:00 each night across six consecutive nesting seasons, from mid-June to the end of October from 2013 to 2018. Fieldwork was carried out by an experienced researcher helped by at least two volunteers. When a nesting loggerhead female was encountered, the team remained behind the turtle until it commenced digging the egg chamber, to minimize disturbance. Clutch size was recorded during oviposition, if possible, or not recorded if oviposition had already begun. The team did not manipulate or touch the eggs, except after hatchling emergence, during the excavation of these nests. Tagging was only conducted after the female finished laying eggs, to prevent disturbing it. Researchers checked for the presence of a Passive Integrated Transponder (PIT) tag in the flippers and neck area using a Mini Tracker III AVID scanner. If a PIT tag was detected, its code was recorded. If the female was not tagged, a new PIT tag was injected into the right front flipper following established protocols (Marco et al., 2012b). The curved carapace length (CCL) was measured for each female using a flexible measuring tape with an accuracy of 2 mm. Positional data (latitude and longitude, coordinate system WGS 1984) were recorded for each nest using a calibrated handheld GPS receiver (Garmin etrex, Garmin LTD, Cayman Islands; accuracy ≤ 4 m).

The locations of 4875 nests (n [2013] = 121, n [2014] = 355, n [2015] = 375, n [2016] = 631, n [2017] = 1145, n [2018] = 2248) were recorded. Differences among the nests recorded was due the number of nesting females present in each season. The vegetation line (VEL) was defined as the line where permanent vegetation started, or as the limit between the sand and the clay at the back of the beach if no vegetation was present. The TIL was defined as the border between wet and dry sand at mid-tide; this was suitable for our study area because Cabo Verde has a low tidal amplitude, with less than one meter for most of the year (Ferreira-Veiga, 2018). The VEL and the tide line (TIL) were mapped on foot whilst holding a GPS receiver. We calculated the minimum linear distance between each one of the nest points and the VEL using QGIS (version 3.8.3) software. For 489 of these nests, we also recorded the distance to the TIL and nest elevation (NEL) (n [2013] = 33, n [2015] = 320, n [2016] = 87, n [2017] = 34, n [2018] = 15). The distance to the TIL was measured with a flexible plastic measuring tape from the water line at the time of data collection (defined as the height of the water at the time of laying, where the female’s track began) to the location of the nest centre. A laser level (Bosch PLL 5 Laser Spirit Level) placed on the beach surface over the nest was used to measure the NEL, with the laser line projected horizontally onto a graduated stick positioned at the water level. When dunes or other objects blocked the illumination of the TIL stick by the laser light, a graduated vertical stick was positioned over the nest and the laser level was elevated until the light was projected on

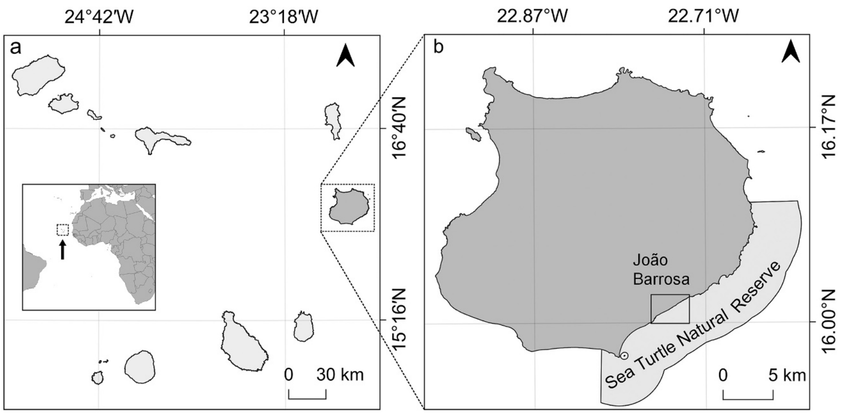

Fig. 1. (A) Map of the Cabo Verde islands, West Africa (inset map shows the location of the Cabo Verde archipelago off the coast of West Africa), and (B) Map of Boa Vista (showed in dark grey inside dashed box in [A]). The location of the João Barrosa beach is inside the frame. Light grey area shows the boundaries of the Sea Turtle Natural Reserve.

the TIL stick. The NEL was calculated by subtracting the height of the laser level over the beach surface from the level of the laser line on the TIL stick. When the distance was too long and the laser line was not visible in the TIL stick, the transect was divided into two or more sectors, and the elevation measured and summed across each. The TIL and NEL measurements were recorded at night, during egg laying.

The complete nesting process was observed for a total of 663 nests (n [2013] = 91, n [2014] = 57, n [2015] = 57, n [2016] = 145, n [2017] = 164, n [2018] = 149), allowing clutch size to be counted. These nests were marked with a numbered stick and monitored daily in the morning and any tidal inundation or predation by ghost crabs was recorded. Ghost crab predation was detected through daily counts of ghost crab burrows on the nests as described in Marco et al. (2015). After the 45th day of incubation, nests were monitored for signs of hatchling emergence, identified by hatchling tracks. Two to three days after emergence, nests were excavated. Nests where emergence was not observed after 60 days of incubation were also excavated. Hatching success (%) was calculated by dividing the number of empty eggshells by the initial number of eggs in the nests (Miller, 1999). Emergence success was calculated as the number of empty eggshells minus the number of live and dead hatchlings inside the egg chamber divided by the initial number of eggs in the nest (Miller, 1999). Eggs were only handled during the excavation process to avoid stimulating ghost crab predation (e.g. through odour release).

2.3. Data analyses

All statistical analyses were performed using the software R v.4.0.0 (R Core Team, 2020), and for statistical tests we assume a 5% level of significance. To investigate trends in nest site selection across the beach and by female body size, we used linear mixed effects models (LMM) with a Gaussian distribution, performed using the "*lmer*" function from the "*lme4*" package (Bates and Bates, 2007), having female identity as a random effect, the VEL, TIL and NEL as response variables (each assessed in a separate model), and including the fixed explanatory factors year (from 2014 to 2018 for VEL and 2016–2018 for TIL and NEL), month of nesting season (from July to September) and female CCL. We then used linear models with the same response variables, but excluding the random effects (i.e. female identity).

Pearson's correlation coefficient was used to analyze whether the distances of the nests to the VEL, the distance of nests to the TIL and the nests NEL were correlated with each other, to avoid collinearity of explanatory variables in our analysis (Supplementary Table A1).

We ran a generalized linear mixed model (GLMM) with a binomial error structure and a logit link function, using the "*glmer*" function, to test if hatching success and emergence success could be predicted from the VEL. The models included female identity as a random effect, and year (from 2016 to 2018), month (from July to September) and female CCL as explanatory factors. We also used generalized linear models (GLM) with the same response and same explanatory variables and excluding female identity.

We performed likelihood ratio and Akaike Information Criterion tests corrected for small sample size (AICc), to see which models better fitted the data (Burnham and Anderson, 2002). The adjusted R-squared (R^2_{adj}) values of models were calculated using the R package "*rsq*" (Zhang, 2021). The significant effects of the retained models were tested using the "*Anova*" function of the "*car*" package (Fox et al., 2013) with type-II sums of squares, using F-tests for the LMM and Wald Chi-square for the GLMM models.

To investigate variation in nest site selection according to female phenotype, the beach was divided into three equidistant sections from the high tide line to the back of the dune vegetation line, using QGIS 3.8.3 software. These beach sections were labelled as "tidal area", "middle of the beach" and "near vegetation". We grouped nests according to their placement on the beach (near vegetation, middle of beach, tidal area). After checking the data for normality (using Shapiro-Wilk's test) and homogeneity of variance (using Levene's test), we tested for differences in the mean size of nesting females between these groups using a Kruskal-Wallis test.

Previous skeletochronology work has indicated that larger females nesting in Boa Vista Island are older than small nesting females in the same beaches (Eder et al., 2012). We therefore used female body size as a proxy for age to infer if turtles with different ages vary in their nesting site selection strategy. Eder et al. (2012) structured size/age-classes of the population as large (older) > 93 cm and small (younger) < 82.5 cm females. Thus, following this classification, we divided females into three size-classes, so that there was a clear separation between small and large. We classified nesting females as large (CCL > 93 cm), medium (93 ≤ CCL ≤ 82.5 cm) or small (CCL < 82.5 cm).

We quantified individual differences in nest-site selection by calculating their repeatability (r) in terms of nest distances to the VEL, TIL and NEL. For repeatability analysis we used the nest locations of loggerhead females that laid ≥ two clutches in a nesting season. The model was performed using the "rptGaussian" function from the "rptR" package (Stoffel et al., 2017), with the 95% confidence interval calculated through parametric bootstrapping using 1000 iterations (Carrasco and Jover, 2003; Nakagawa et al., 2010). Repeatability analysis for Gaussian data (distance to the VEL, distance to the TIL and NEL), estimates the repeatability from a general linear mixed-effects model fitted by restricted maximum likelihood (Carrasco and Jover, 2003; Nakagawa et al., 2010). We conducted the repeatability analysis first for all females across all sizes and then for females within each size class.

3. Results

The 4875 nests that we recorded across the study period corresponded to 3880 individually identified loggerhead turtles. Most females were observed nesting only once ($n = 3112$), and a total of 768 females were recorded nesting more than once (twice [$n = 577$], three times [$n = 145$], four [$n = 35$], five [$n = 7$], six [$n = 2$], seven [$\mathrm{n} = 1$] and eight [$\mathrm{n} = 1$] times) over the six-year study period. The number of nests observed per female during the same season ranged from one to six. Females selected nesting sites from below the high tide line to beyond the VEL (Fig. 2; Supplementary Fig. A1). João Barrosa beach is on average 75.4 m (95% Confidence Intervals CI = 75.2, 75.7) wide, ranging from 32.3 to 161.1 m.

When we divided the beach in three equidistant sections from the high tide line to the back of the dune vegetation line, the nests were not homogeneously distributed across theses sections ($X^2 = 13.2$, $df = 2$, $p = 0.0014$). Most (48.7%) nests were concentrated in the middle of the beach, i.e. open beach, whilst 32.2% and 19.1% were located near vegetation and tidal area, respectively.

The mean distance of nests to the VEL was 25.2 m (CI = 24.7, 25.8, $n = 4875$), ranging from −23.2 to 92.6 m (Supplementary Fig. A2.a). The mean distance to the TIL was 29.7 m (CI = 28.4, 31.0, $n = 489$), ranging from −2.0 to 97.0 m (Supplementary Fig. A2.b) and the mean NEL was 0.8 m (CI = 0.7, 0.8, $\mathrm{n} = 489$), ranging from −0.3 to 2.9 m (Supplementary Fig. A2.c). A *t*-test analysis showed a significant difference between the distribution of the nest distance to VEL and the distribution

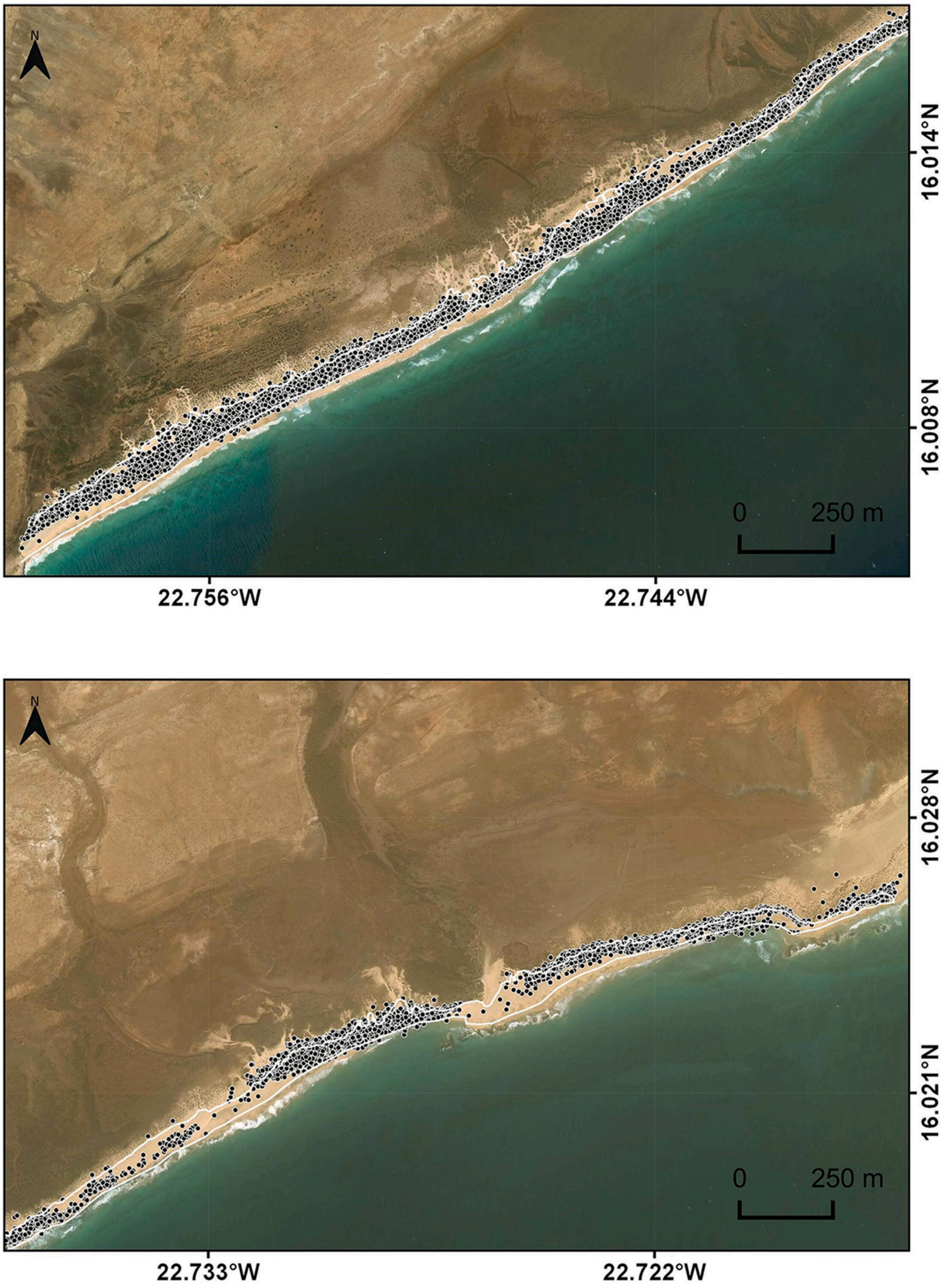

Fig. 2. Aerial photo of João Barrosa beach (Boa Vista Island, Cabo Verde). The black dots show the location of loggerhead turtle nests, while the white lines delimit both the vegetation zone and the tide line. The image was divided in half in order to zoom.

of the nest distance to TIL ($t = 4.1496$, df $= 212.24$, $p < 0.0001$, CI $=$ 2.7–7.5). Negative values correspond to nests located on the back of the beach beyond the VEL (distance to VEL) and in areas below sea level (NEL). Of all nests recorded, 7.7% ($n = 373$) were within the vegetation. Of the nests for which we recorded the distances to the tide line and elevation, 28.6% ($n = 140$) were < 20 m from the tide line, 26.7% ($n = 130$) were < 0.5 m in elevation and 60.5% ($n = 296$) of the nests were < 1 m in elevation.

There was no significant relationship between any pair of the 3 variables (VEL, TIL and NEL; Supplementary Table A1). All models had limited explanatory power (R^2_{adj} values of 0.03–0.39; Table 1). For VEL, the best-fitting model included the predictor variables female CCL, month, year and female identity as a random effect (Table 1). We found a significant effect of the variable month ($F_{(2,\ 1426)} = 6.27$, $p = 0.002$), with nests closer from the VEL during the September, a marginally significant of year ($F_{(3,\ 954)} = 3.29$, $p = 0.020$), but not significance effect of the female CCL ($F_{(1,\ 690)} = 3.22$, $p = 0.073$).

The best-fitting model for distances to the TIL also included female CCL, month, year and female identity as a random effect (Table 1), but only female CCL presented marginally significant effects ($F_{(1,\ 57)} = 4.27$, $p = 0.043$), with larger females tending to nest further from the TIL. The year ($F_{(1,\ 83)} = 1.15$, $p = 0.335$) and months ($F_{(4,\ 122)} = 1.29$, $p = 0.277$) were not statistically significant. The best-fitting model for NEL data excluded female identity as a random effects (Table 1), but we did not find support for statistically significant effects of any variables.

Of the monitored nests ($n = 663$), 70.3% ($n = 466$) suffered total mortality, of which 63.3% ($n = 420$) suffered confirmed ghost crab predation and 49.6% ($n = 329$) were inundated by the tide. Some nests ($n = 173$) suffered predation by ghost crabs and were flooded. All models relating hatching and emergence success to the measured variable distance to VEL including female identity as a random effect showed moderate R^2_{adj} values (0.67–0.68; Table 2). The models that best fit both datasets (hatching and emergence success) included the female identity as a random effect (Table 2), and all the covariates present statistically significant effects ($p < 0.0001$; Table 3). Overall mean hatching success was 33.2% ($SD = 38.4$) and emergence success was 30.0% ($SD = 37.2$). Both hatching and emergence success were lower in July (hatching: mean $=$ 22.9%, SD $=$ 34.0; emergence: mean $=$ 20.6%, SD $=$ 32.9; Fig. A3) and 2016 was the year with lower success (hatching: mean $=$ 32.7%, SD $=$ 38.9; emergence: mean $=$ 27.9%, SD $=$ 37.2). The success tends to decreased with female CCL and with distances from nests to the vegetation line (Table A2).

There were no differences in mean size of nesting females between nests deposited close to the vegetation, in the middle of the beach or in the tidal zone (Kruskal-Wallis test: $H_2 = 2.55$, $p = 0.28$).

There was significant repeatability in the distance to the VEL ($r = 0.12$, SE $= 0.03$, CI: 0.07–0.18, $p < 0.0001$, $n = 768$ turtles and 1791 clutches). Repeatability in the distance to the TIL or on NEL was not significant, with values approaching zero. When assessing repeatability with respect to the size-class of the nesting female in relation to distance from the vegetation, larger females (CCL $>$ 93 cm) showed higher repeatability in nest placement compared to other size-classes ($r = 0.50$, SE $= 0.14$, 95% CI: 0.16–0.72, $p < 0.0001$; $n = 19$ turtles and 59 clutches, Fig. 3). Medium (CCL 82.5–93 cm) and small (CCL $<$ 82.5 cm) females showed significant repeatability in the distance to the VEL, but to a lesser extent (medium: $r = 0.11$, SE $= 0.05$, 95% CI: 0.02–0.20, $p < 0.001$, $n = 325$ turtles and 745 clutches; small: $r = 0.07$, SE $= 0.04$, 95% CI: 0.0–0.15, $p < 0.05$, $n = 424$ turtles and 987 clutches). We were unable to assess if repeatability in distance to the TIL and in NEL varied between size-classes due to small sample sizes.

4. Discussion

In this study, we explored the spatial distribution of loggerhead turtle nests across the beach profile, evaluated the effect of nest location on hatching and emergence success, and investigated nest site selection in nesting females of one of the largest loggerhead turtle rookeries in the world, the North East Atlantic subpopulation. Although the study focused on one beach, this area covers 20% of the entire population's nesting activities (Marco et al., 2012a). Overall, repeatability of nest site selection was low, yet much higher among larger and older turtles (CCL $>$ 93 cm).

Overall, female identity was an important predictor of both the nest site selection and of hatching and emergence successes, only with the exception of nest elevation, suggesting that some of the variability observed in these parameters is intrinsic to individuals. We found however some patterns at the population level, for instance whilst loggerhead females from João Barrosa beach nest across all zones of the beach, including beyond the vegetation line and below the tidal zone, they preferentially nested on the open beach, mostly in the middle of the beach width, avoiding to nest both close to the tideline and close to the vegetation line. The preference for the open beach in João Barrosa is consistent with that reported for other loggerhead turtle populations (Hays and Speakman, 1993; Karavas et al., 2005; Hatase and Omuta, 2018). Clumping nests away from the sea seems to be effective in protecting the eggs from flooding or loss to beach erosion (Wood and Bjorndal, 2000; Kamel and Mrosovsky, 2004; Hatase and Omuta, 2018; Martins et al., 2022). The lower occurrence of nesting close or within the vegetation may be due to digging impediment by roots (Hays and Speakman, 1993; Karavas et al., 2005), or due to drier sand (Martins et al., 2022), which makes it difficult for females to dig the nest. In addition, hatchlings emerging in the back of the beach, close to the vegetation may be less likely to reach the sea (Hays and Speakman, 1993; Kamel and Mrosovsky, 2004; Martins et al., 2021a). The vegetation in Boa Vista beaches may be playing an important role as an environmental cue to guide females' nest site choice, also limiting them from

Table 1
Comparison of best-fitting linear mixed models and linear models fitted to nest distance to the vegetation line, nest distance to the tide line and nest elevation data, including female CCL, year and months as predictor variables and having female identity as a random effect. For each model the degrees of freedom (df), Akaike information criterion (AICc), the change in AIC relative to the best model (ΔAIC), the model weight (AIC wt), the Log-likelihood (LogLik) and adjusted R-squared (R^2_{adj}) are given.

Response	Model terms	df	logLik	AICc	ΔAICc	AIC wt	adjusted R^2_{adj}
Distance to vegetation	CCL + months + years +1|female ID	10	−7351.5	14,723.1	0	0.989	0.15
	CCL + months +1|female ID	5	−7361.2	14,732.5	9.4	0.009	0.15
	Months +1|female ID	6	−7361.7	14,735.5	12.4	0.002	0.15
	CCL + months + years	9	−7365.6	14,749.3	26.2	<0.001	0.02
Distance to tide	CCL + months + years +1|female ID	11	−568.0	1160.0	0	1	0.39
	CCL + months +1|female ID	8	−578.6	1174.3	14.3	<0.001	0.39
	CCL + years +1|female ID	7	−580.4	1175.7	15.7	<0.001	0.39
	CCL + months + years	10	−590.5	1202.6	42.6	<0.001	0.12
Height	CCL + months + years	10	−118.9	259.5	0	0.9866	0.07
	Months +1|female ID	7	−126.8	268.4	8.9	0.0113	0.03
	Months + years +1|female ID	10	−125.1	271.7	12.3	0.0022	0.07
	CCL + months + years +1|female ID	11	−128.8	281.6	22.1	<0.001	0.07

Table 2

Comparison of best-fitting generalized linear mixed models and generalized linear models fitted to hatching and emergence success data, including nest distance to vegetation line (VEL), female CCL, clutch size, year and month as predictor variables, and having female identity as a random effect. For each model the degrees of freedom (df), Akaike information criterion (AICc), the change in AIC relative to the best model (ΔAIC), the model weight (AIC wt), the Log-likelihood (LogLik) and adjusted R-squared (R^2_{adj}) are given.

Response	Model terms	df	logLik	AICc	ΔAICc	AIC wt	adjusted R^2_{adj}
Hatching success	VEL + CCL + months + years +1|female ID	8	−3259.4	6535.2	0.0	1	0.68
	VEL + CCL + months +1|female ID	6	−3354.1	6720.5	185.3	<0.001	0.68
		7	−9408.1	18,830.6	12,295.4	<0.001	0.12
Emergence success	VEL + CCL + months + years +1|female ID	8	−3159.9	6336.4	0.0	1	0.67
	VEL + CCL + months +1|Female ID	6	−3240.2	6492.8	156.4	<0.001	0.67
	VEL + CCL + months + years		−8945.5	27,906.4	11,569	<0.001	0.10

Table 3

Analysis of deviance summary table (Type II Wald chi-square tests) for generalized linear mixed models to test for correlations between nest distance to the vegetation line [VEL], female CCL, clutch size, year and month (predictor variables) and hatching success and emergence success, having female identity as a random effect.

Response variable	Predictor variables	X^2	Df	*p*
Hatching success	VEL	57.01	1	< 0.0001
	Female CCL	252.48	1	< 0.0001
	Year	178.10	2	< 0.0001
	Months	1102.24	2	< 0.0001
	VEL	52.20	1	< 0.0001
	Female CCL	210.37	1	< 0.0001
	Year	153.46	2	< 0.0001
Emergence success	Months	952.23	2	< 0.0001

crawling inland and strand. At João Barrosa (and throughout the STNR), there is a muddy area at the back of the beach, behind the vegetation line, and females that are stranded in the mud cannot return to the sea, so they are often rescued. This only occurs at sites where the coastal vegetation breaks, and turtles can access the muddy area, demonstrating the important role of vegetation as a spatial and environmental cue for nest site selection in this population.

We observed that hatching success tended to decreased with distance from the vegetation border, but the power of our models (R^2_{adj}) was not high. This trend may therefore be also due to the high variability of individual females, and potentially to factors not explored in this study, such as microorganism infection (Sarmiento-Ramírez et al., 2010), ghost crab predation (Marco et al., 2015; Rodrigues et al., 2016; Martins et al., 2021b) or other environmental factors that can be influenced by clutch position on the beach such as sand temperature, moisture or texture (Karavas et al., 2005; Abella et al., 2016; Martins et al., 2022). Other work has found that nests close to the vegetation line are less exposed to tidal inundation (Wood and Bjorndal, 2000; Kamel and Mrosovsky, 2004). This was not the case at João Barrosa beach, however, due to its low elevation profile, with the highest nest elevation recorded in this study being 2.9 m, and 60% of recorded nests being below 1 m elevation. Furthermore, despite the fact that ghost crabs on Boa Vista Island occur more in the intertidal zone, 9–13 m distance from the tide line (Martins et al., 2021a), predation occurs across the entire beach profile (Marco et al., 2015; Rodrigues et al., 2016; Martins et al., 2021b). Therefore, the risk of inundation and predation remained high, regardless of distance from the tide line.

Higher hatching success closer to the vegetation border has been observed in other sea turtle populations (Karavas et al., 2005; Liles et al., 2015; Hatase and Omuta, 2018), whilst, conversely, lower hatching success has been reported for other populations. For instance, populations of leatherback sea turtle in the US Virgin Islands that demonstrate the former (Conrad et al., 2011) and hawksbill sea turtles in Antigua Islands, West Indies that demonstrate the latter (Ditmer and Stapleton, 2012). This contradiction may result from differences in vegetation type with different levels of shade and moisture retention, or to the presence of microorganisms in the soil, which can also have a negative effect on hatching success (Sarmiento-Ramírez et al., 2010; Ditmer and Stapleton, 2012).

Hatching and emergence success were lower in July, which typically coincides with a period of heavy rainfall and high spring tides in Boa Vista, leading to high mortality of clutches, (Martins et al., 2021b). The effect of female CCL on hatching success and emergence success (Table A2) may be indirectly related to nest placement with respect to distance from vegetation than a morphological feature of female (in this case, the body size). The effect of year could be due to factors operating at inter annual scales, such as variation in sand temperature, moisture or tide regimes (Abella et al., 2016; Marco et al., 2017; Martins et al., 2022) not considered here. The year 2016 was the season with lower nesting activities (compared with 2017 and 2018 season) and was the year worst success, and a potentially cause of this lower success may be related to the rate of predation by ghost crabs. In the season with low nesting activities, the impact of ghost crab's predation can be severe, compared to seasons with more abundance of nests. We suggest that further studies include these variables.

Overall, loggerhead turtles in João Barrosa beach showed a low consistency in nest site selection at the spatial scales that we explored in terms of distances to the vegetation, the tide line or nest elevation. A lack of a clear trend in nest site selection has previously been reported at a loggerhead turtle rookery on Mon Repos beach, Australia, where females did not consistently select nest sites at particular distances from the stationary dune baseline (Pfaller et al., 2009), in leatherbacks turtles at Playa Grande, Costa Rica (Nordmoe et al., 2004), and at Awa:la-Ya: lima:po, French Guiana (Kamel and Mrosovsky, 2004). However, this pattern differs from studies conducted in other species such as green turtles in Guinea-Bissau (Patrício et al., 2018), and hawksbill turtles in Guadeloupe (Kamel and Mrosovsky, 2006), El Salvador and Nicaragua (Liles et al., 2015), where a high consistency in nest-site choice in relation to the overstory vegetation cover (repeatability, $r > 0.5$) was reported. This suggests that sea turtle populations present higher interspecific differences in nest site selection than intraspecific differences (Nordmoe et al., 2004; Pfaller et al., 2009).

Nonetheless, our results showed that larger females were more consistent in their nesting site selection in distances to the vegetation line than smaller females. Assuming that larger sized turtles are older (Eder et al., 2012), such observations may be related to experience that individuals develop with age. Considering that sea turtles do not possess information on offspring success rates, females may become habituated to a particular nesting location on the beach based on the successful completion of nesting within and across seasons (Pfaller et al., 2009; Patrício et al., 2018). This could explain why larger (and hence older) females become more consistent in their nest site selection. As the relationship between size and age is not linear in sea turtles, a study assessing nest site repeatability between remigrants and recruits would help to test (and eventually support) the hypothesis of experience-related nest site repeatability.

If nest site selection is, at least partially, driven by age and experience, it supports the hypothesis that alternative life histories observed in sea turtle populations may derive from phenotypic plasticity and not necessarily from a genetic basis (Pfaller et al., 2009; Santos et al., 2016;

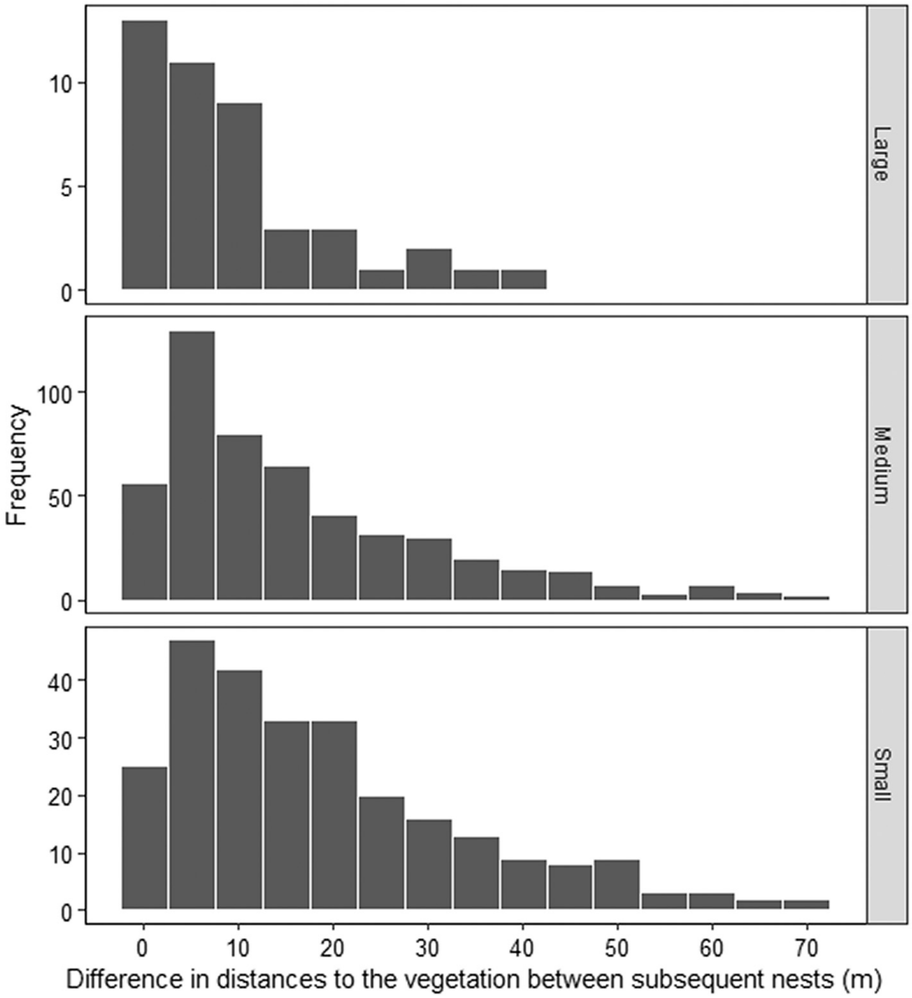

Fig. 3. Frequency distribution of differences in distance to the vegetation line between two consecutive nests of the same loggerhead turtle (*Caretta caretta*) in João Barrosa beach (Boa Vista Island, Cabo Verde). Females were grouped in different size classes: Large (CCL > 93 cm), medium (93 ≤ CCL ≤ 82.5 cm) and small (CCL < 82.5 cm).

Hatase and Omuta, 2018). Previous studies have suggested that variation between females may have a genetic basis and that nest site selection may thus be a heritable trait (Kamel and Mrosovsky, 2004, 2006), yet other researchers suggest that female turtles exhibit local adaptations likely dependent on the dynamic of the nesting beaches (Nordmoe et al., 2004; Pfaller et al., 2009; Liles et al., 2015). The Sea Turtle Natural Reserve coast at Boa Vista is characterized by highly dynamic beaches, including João Barrosa, with frequent flooding events and erosion caused by high tides and heavy rain. Nest site selection in dynamic beach environments where nest mortality is unpredictable, would favor a strategy of scattering reproductive effort, thus increasing the probability that at least some nest sites will be successful (Eckert, 1987; Pfaller et al., 2009).

Conservation implications.

Our results have important implications for sea turtle conservation in Cabo Verde. We recommend protecting the beach vegetation from coastal development, as it may be a cue in nest distribution. This is also an important lesson for other nesting beaches of the Cabo Verde archipelago. For instance, in Sal Island, the most touristic and one of the most important islands for loggerhead turtle conservation in Cabo Verde (Laloë et al., 2019) there is significant pressure for coastal development and for touristic activities that may destroy the beach vegetation.

Due to the high natural nest mortality rate in the Sea Turtle Natural Reserve (Marco et al., 2015, 2017) clutches are frequently relocated to a protected hatchery (Martins et al., 2021b). However, clutch relocation to hatcheries is controversial, as it may distort gene pools (Mrosovsky, 2006; Pike, 2008; Pfaller et al., 2009), and there remains no consensus on whether relocation is an effective conservation tool for sea turtles. This is because it is speculated that if females consistently select nesting sites in a given zone of the beach, nest-site selection may be considered a heritable trait (Mrosovsky, 2006), hence, relocation of doomed clutches may be artificially selecting for turtles that make poor nesting site selections and hence distorting natural gene pools (Kamel and Mrosovsky, 2006; Mrosovsky, 2006). However, we report here that individual loggerhead turtles in João Barrosa beach show low consistency in nest site selection. This can be understood as a high phenotypic adaptive capacity of the population (Abella et al., 2010). Plasticity in nest placement has been observed elsewhere in Cabo Verde, as some loggerhead females have been observed nesting at different beaches and different islands with variable topography and different micro-habitats (Abella et al., 2010). Therefore, nest relocation is likely not detrimental to the gene pool of the loggerhead turtle population in the Sea Turtle Natural Reserve, and could continue to be used as a tool to increase hatchling production and enhance population recovery.

Author contributions

SM AM conceived the ideas, designed methodology and collected the data; SM NL and RP analysed the data. The first draft of the manuscript was written by SM, with all authors contributing to the final draft and approving it for submission. All authors contributed to the article and approved the submitted version.

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Declaration of Competing Interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2022.151798.

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