Strategic nest site selection in one of the world's largest loggerhead turtle nesting colonies, on Maio Island, Cabo Verde

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Abstract For species without parental care, such as sea turtles, nest site selection is particularly important for embryo development, hatchling survival and, ultimately, reproductive success. We conducted an 8-year (2012–2019) capture–mark–recapture study of the re-nesting behaviour of loggerhead turtles *Caretta caretta* to identify both inter- and intra-beach patterns of nest site selection. Our study site, Maio Island in the archipelago of Cabo Verde, hosts one of the largest loggerhead turtle nesting colonies globally. Of 1,060 females analysed, 77% laid repeated clutches within 15 km of their previous nesting sites both between and within nesting seasons. This site fidelity was particularly high (64–71%) for turtles nesting on the east coast of Maio Island. In two areas of the island (north-west and south-east) individual nesting zone consistency was extremely low (10–25%). In all cases extra-zone re-nesting events mainly occurred on the east coast. We also found that females avoided re-nesting near the shoreline, which is particularly relevant in the context of rising sea levels. Overall, loggerhead turtles nesting in Maio Island are philopatric but are using a bet-edging strategy to distribute nests amongst several beaches, choosing the safest area within each beach to maximize their reproductive success. This study highlights the priority sites for protection on Maio Island and could help to optimize capture–mark–recapture programmes. The data reveal the potential for adaptive responses to projected sea level rises.

Keywords Cabo Verde, *Caretta caretta*, conservation management, nesting behaviour, philopatry, plasticity, sea-level rise, sea turtle

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Introduction

Philopatry, the return to a natal place to breed, is a common life-history strategy used by both terrestrial and aquatic species (Koenig et al., 1996), including sea turtles. They often follow circuitous routes during their migrations, but despite this crude map sense in the open ocean, they can find the oceanic islands where they were born and that they will use to nest (Hays et al., 2020).

Once in their natal area, turtles are faced with dynamic beaches that can vary in terms of morphology, type of sand and vegetation (Conrad et al., 2011; Ditmer & Stapleton, 2012). Because of their use of bet-edging strategies or because of their inaccurate navigation mechanisms some females distribute their nests amongst several beaches (Weishampel et al., 2003; Kamel & Mrosovsky, 2004).

In sea turtles there is no parental care for the eggs or the hatchlings and therefore the selection of both a particular beach and the microhabitat within a beach determines hatching success, the physical condition of the hatchlings (Patrício et al., 2018), the reproductive fitness of the adults, and subsequently the survival of the population (Hays & Speakman, 1993). Clutches deposited near the ocean are more likely to be lost because of erosion and flooding, whereas nest placement further inland leads to a greater likelihood of hatchling misorientation and in some colonies greater predation (Wood & Bjorndal, 2000; Caut et al., 2010; Patino-Martinez et al., 2017). In some turtle species, nests located in open sand areas have also been observed to produce more viable hatchlings per clutch than nests located under vegetation (Ditmer & Stapleton, 2012). The variable environmental conditions in the nests during incubation induce variation in the phenotypes, sex and vitality of the hatchlings (Ditmer & Stapleton, 2012; Patino-Martinez et al., 2014; Kobayashi et al., 2017).

Here we describe the degree of nesting beach selection and the consistency of intra-beach site selection for egg deposition over 8 years in one of the largest loggerhead turtle *Caretta caretta* colonies: Maio Island on Cabo Verde, West Africa (Cozens et al., 2011; Dutra & Koenen, 2014; Patino-Martinez et al., 2022a). In the last decade (2012–2021) the number of nests has increased on Maio Island, with a mean of 19,415 ± SD 16,450 nests per season during 2017–2021 (Patino-Martinez et al., 2022b).

The loggerhead turtle is categorized as Vulnerable on the IUCN Red List and its persistence is considered to be conservation-dependent (Casale & Tucker, 2017). The subpopulation of Cabo Verde has been identified as genetically separate from other loggerhead turtle stocks (Monzon-Arguello et al., 2010; Wallace et al., 2010; Stiebens et al., 2013), with multiple genetic groups in the rookery (Stiebens et al., 2013; Baltazar-Soares et al., 2020). This subpopulation is categorized as Endangered based on IUCN Red List criterion B2 because of the continuing decline in area, extent and/or quality of its habitat (Casale & Marco, 2015).

Maio Island is heterogeneous and the characteristics of its nesting beaches vary throughout the island in terms of dimension, slope, colour, composition and temperature of the sand, providing a variety of microhabitats for nest incubation (Patino-Martinez et al., 2022b). In this study we (1) investigated the re-nesting beach consistency across the entire island and (2) evaluated the consistency of intra-beach nest site selection for three beach areas with different flood risks. The results of this study will help prioritize areas of conservation importance, optimize capture–mark–recapture programmes and evaluate the potential for adaptive responses to projected sea-level rises (Fuentes et al., 2010).

Study area

Maio Island (Fig. 1) in the Republic of Cabo Verde, West Africa, is 269 km² (24 km long × 16 km wide) and hosts nesting loggerhead turtles on sandy beaches that cover 35 km of its 117.8 km of coastline. At present, the high-energy beaches of Maio Island are largely undeveloped, with low anthropogenic impacts resulting in near-pristine habitat. The colour and temperature of the sand, the dimensions, slope and bathymetry of the beaches and the natural hatching success rates vary greatly throughout the island (Patino-Martinez et al., 2022a). The nesting season is mid June–mid November, with a peak in August.

Methods

Geographical distribution of nesting Nesting is distributed around the whole island. For the purposes of this study, the island was divided into eight geographical areas (each c. 13 km long) according to the eight points of the compass (Fig. 1). Loggerhead turtle nesting habitats (sandy beaches) available and monitored in each area were 2.4 km (in the east-north-east) to 8.0 km (in the south-south-west) long. We monitored 63,101 loggerhead turtle nesting activities (aborted nesting attempts and successful nesting) in all eight areas over eight nesting seasons (2012–2019) during July–October. We tagged the 7,872 monitored turtles with either PIT tags on the right shoulder, metal tags on both front flippers or using both methods, following recommended sea turtle tagging protocols (Balazs, 1999). We recorded the location of each nesting activity of each female using a GPS, and set the maximum possible observed distance of nest scattering to c. 52 km. We did not examine inter-island nest scattering.

Intra-beach nest site selection During 2017–2019 we studied the intra-beach locations of 2,769 pairs of nests of females for which we recorded at least two nests (excluding aborted nesting attempts) within a nesting season. We cannot exclude the possibility that turtles could have nested between recorded events. We classified the distribution of nests according to their location in three different zones associated with varying levels of flood risk: high, medium and low. The high-risk zone covers the nesting area below the high water mark, the medium-risk zone represents that between the high tide line and where dune vegetation begins, and the low-risk zone corresponds to the area above the dune vegetation line extending to the back of the beach. We measured the widths of the three zones simultaneously (1 h after low tide) at six reference beaches. For the null model we calculated the expected number of nests as a function of the mean area of each zone, assuming equal density across zones.

Data analyses We aggregated all unique tag records and organized them chronologically. We combined the information regarding tagged nesting females and geographical areas or intra-beach flood risk zone to produce a from–to relation matrix for geographical area/flood risk zone re-nesting preferences. If the starting geographical area (y axis) and the destination geographical area (x axis) were the same, this implies that the female returned to the same zone in the following observed nesting event (Table 1). We calculated the per cent of re-nesting events in the same area (column R in Table 1). The remaining from–to cells represent the tendency to choose different geographical areas in two sequentially observed nesting events. The number in each cell indicates the number of repetitions of each specific re-nesting behaviour (Table 1). To determine the re-nesting site selection consistency at both study scales (geographical area and intra-beach microhabitat) we ran χ^2 goodness-of-fit tests for observed counts that included the analysis of specific proportions of nests per geographical area or microhabitat. We analysed successful nests and nesting attempts separately, and analysed observations of re-nesting both within and between nesting seasons. Statistical significance was set to $P < 0.05$ and values reported are means ± 1 SD.

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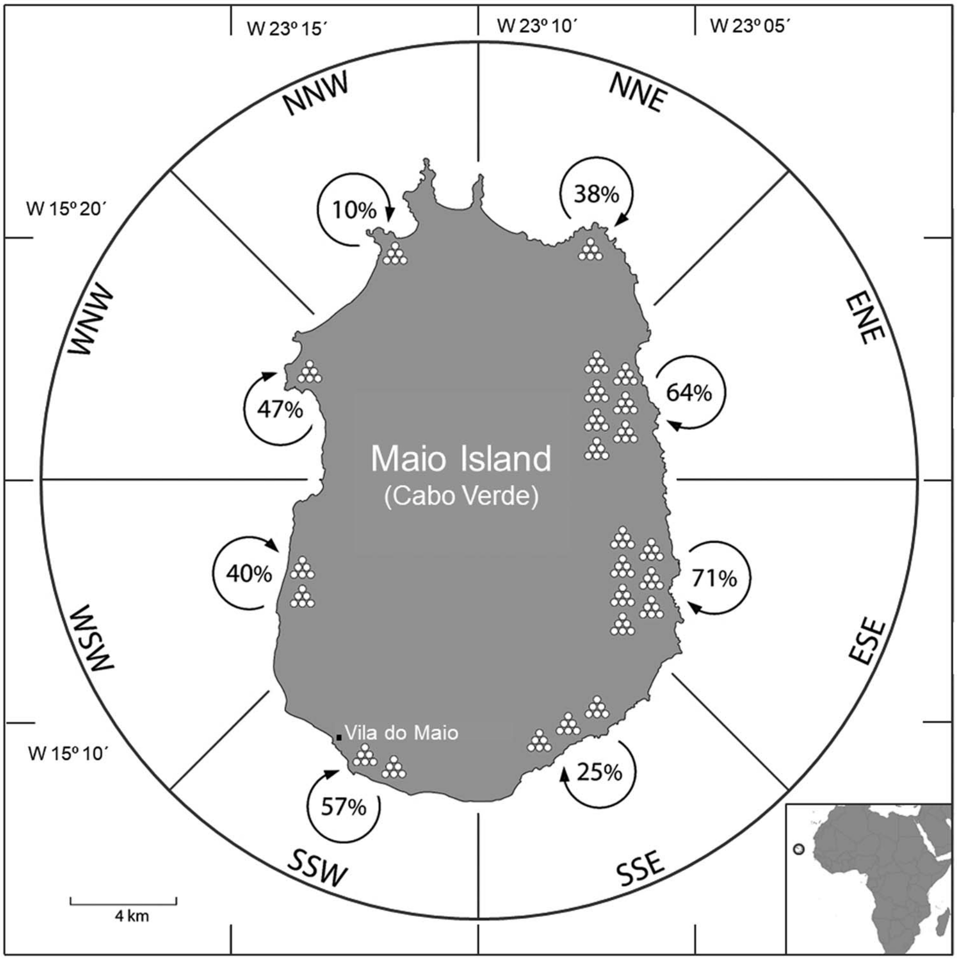

FIG. 1 Maio Island, Cabo Verde, West Africa, showing the eight geographical divisions according to the eight points of the compass, used to examine consistency in loggerhead turtle *Caretta caretta* nesting site selection. Nesting habitats (km of sandy beaches) available and monitored in each study area were NNE = 3.3, ENE = 2.4, ESE = 2.5, SSE = 3.6, SSW = 8.0, WSW = 6.2, WNW = 2.6 and NNW = 6.2. The per cent values within the curved arrows indicate the observed re-nesting rates within each of the eight areas. The pyramids of circles represent the relative abundance of loggerhead turtle nests (one pyramid, < 5%; two pyramids, 5–10%; three pyramids, 10–15%; seven pyramids, 30–35%). The circle on the inset map shows the location of Cabo Verde off the West African coast.

TABLE 1 Loggerhead turtle *Caretta caretta* nesting zone selection matrix on Maio Island, Cabo Verde, during 2012–2019. The island was divided into eight geographical areas according to the eight points of the compass (Fig. 1). 'From' is the first nesting area chosen by a single female. 'To' is the location of the next nesting record for the same female. The number in each cell indicates the number of events of each specific behaviour. R is the per cent of re-nesting events in the same area; n is the absolute number of re-nesting events per area. The diagonal line of cells highlighted in dark grey indicates the number of re-nesting events in the same area. The cells highlighted in light grey indicate the most commonly chosen new area in each case (note that the selection of new sites is mostly on the east coast at ENE and ESE).

	To									
From	NNE	ENE	ESE	SSE	SSW	WSW	WNW	NNW	R (%)	n
NNE	3	3	1	1	0	0	0	0	37.5	8
ENE	1	601	244	35	26	15	8	4	64.3	934
ESE	1	173	662	27	42	11	10	8	70.9	934
SSE	0	71	95	77	45	10	5	2	25.2	305
SSW	0	19	34	29	129	10	5	0	57.1	226
WSW	0	35	29	16	24	83	19	2	39.9	208
WNW	0	14	17	6	1	12	45	0	47.4	95
NNW	0	16	17	3	6	9	2	6	10.2	59

Results

Geographical distribution of nesting We observed 34,253 aborted nesting attempts and 28,848 successful nesting events at Maio Island during 2012–2019. Of the 1,060 females monitored that had three or more re-nesting activities, 77% dispersed their nests by up to 15 km (Table 2) both between and within nesting seasons. Female loggerhead turtles did not re-nest randomly in the different geographical areas of the island, but tended to re-nest frequently on the east coast of the island (east-south-east 70.9% and east-north-east 64.3%) and less frequently elsewhere (north-north-west

TABLE 2 Nest scattering distance (km) in female loggerhead turtles for which at least three nesting events were observed on Maio Island, Cabo Verde, during 2012–2019.

Distance of re-nesting events (km)	No. of females (%)
0.00–0.99	169 (15.9)
1.00–4.49	323 (30.5)
4.50–14.99	327 (30.8)
15.00–52.00	241 (22.8)

10.2% and south-south-east 25.2%; $\chi^2 = 127.09$, df = 7, $P < 0.0001$, n = 1,606; Fig. 1, Table 1). Females that changed areas between successive nests most often moved to the east coast (Fig. 1, Table 1). Analysis of recaptured females between different nesting seasons demonstrated a similar rate of re-nesting in the same area (187/286 = 65%) to recaptured females within the same nesting season (1,606/2,769 = 58%; $\chi^2 = 3.89$, df = 1, P = 0.05, n = 2).

Intra-beach nest site selection The mean width of the study zones was 11.8 ± SD 7.6 m (38.3%) for the high-risk flood zone, 6.8 ± SD 3.7 m (22%) for the medium-risk flood zone and 12.2 ± SD 4.2 m (39.6%) for the low-risk flood zone. Female loggerhead turtles did not re-nest randomly across the three flood risk zones; both those that re-nested in the same geographical area and those that changed area tended to re-nest disproportionately in the medium-risk zone (Table 3). Re-nesting proportions differed significantly amongst the flood risk zones (same geographical area $\chi^2 = 59.89$, df = 2, $P < 0.0001$, n = 762; different geographical areas $\chi^2 = 62.45$, df = 2, $P < 0.0001$, n = 459), being lower in the high-risk zone. In contrast, the proportions of females re-nesting within the low-risk and medium-risk zones were much greater than expected (Table 3).

Discussion

Geographical distribution of nesting

We conducted a comprehensive 8-year survey of individual re-nesting site selection in one of the most important loggerhead turtle nesting colonies, on Maio Island, Cabo Verde (Patino-Martinez et al., 2022a). The study focused on the regional and intra-beach spatial scales.

Our findings confirm that loggerhead turtles tend to have lower beach fidelity and use broader environmental niches than other sea turtle species (Dodd, 1988; Hays & Sutherland, 1991; Pike, 2013). We found that re-nesting site selection within the same geographical area (not always on the same beach) accounts for 58–65% of re-nesting events. This is consistent both within and between nesting seasons, supporting the theory of consistent inter-seasonal nest site selection (Miller, 1997). Approximately 77% of the total number of nesting females laid their nests within 15 km of their previous nests.

TABLE 3 Observed and expected numbers of re-nesting events between intra-beach flooding risk sections used by loggerhead turtles on Maio Island, Cabo Verde. 'From' is the flood risk zone (low, medium or high) selected by females for one nesting event and 'To' is the location of the next nesting event. Re-nesting events within and between geographical areas are shown separately.

Flooding risk		Expected	Observed				
From	To	no. of nests	no. of nests	n	χ^2	df	P
Re-nesting in the same geographical area							
Low	Low	250.9	356	632	239.6	2	< 0.0001
	Medium	139.0	222				
	High	242.1	54				
Medium	Low	296.9	303	748	416.7	2	< 0.0001
	Medium	164.6	371				
	High	286.5	74				
High	Low	89.7	81	226	104.6	2	< 0.0001
	Medium	49.7	110				
	High	86.5	35				
Re-nesting in a different geographical area							
Low	Low	153.6	190	387	181.6	2	< 0.0001
	Medium	85.1	167				
	High	148.2	30				
Medium	Low	215.1	219	542	210.2	2	< 0.0001
	Medium	119.2	244				
	High	207.5	79				
High	Low	92.9	103	234	105.4	2	< 0.0001
	Medium	51.4	106				
	High	89.6	25				

Nest site fidelity has been associated regularly with high-accuracy philopatric behaviour of sea turtles (Broderick et al., 2007; Lee et al., 2007) and this has also been reported for the rookery (Baltazar-Soares et al., 2020).

However, random individual nesting patterns were observed, with only 16% of the re-nesting events occurring within 1 km of the previous nests; re-nesting between different beaches was common. Some re-nesting events during the same season have been recorded between different Cabo Verdean islands that are separated by hundreds of kilometres (J. Patino-Martinez, pers. obs., 2021). We hypothesize that low beach fidelity could be a mechanism to increase the likelihood of placing some nests in environmentally suitable areas. This could increase the potential of loggerhead turtles to adapt to changing environments (Carreras et al., 2018). Beaches on Maio Island and elsewhere are often dynamic and their environment may not be predictable from one nesting event to the next (Kelle et al., 2007). Therefore, once the females are in the nesting area random beach selection could reduce the energetic cost of searching for a particular beach, the characteristics of which may not be stable and thus may not always be suitable for nesting.

We found that nesting females have high-preference and low-preference areas where they consistently re-nest or avoid re-nesting, respectively. Females exhibited high nesting zone consistency (64–71%) on the east coast of Maio Island even though this area had the lowest availability of nesting habitat. The high-preference areas could be a result of the clustering of conspecifics and hence higher chance of finding a mate (Shimada et al., 2021) or of other as yet unknown factors. In two areas (north-north-west and south-south-east) there was low individual re-nesting zone consistency (10–25%). In these areas, and also in the rest of the island, the turtles who chose to re-nest in another area mainly did so on the east coast (the high-preference areas). The geographical areas of low preference coincide with a greater presence of people (poachers and rangers) on the nesting beaches (south-south-east) and more difficult access to the beach from the sea, with shallow waters (north-north-west). These and other parameters used as predictors of re-nesting preference should also be assessed in future studies (Mazaris et al., 2006).

The available nesting sites on the island are generally suitable for embryonic development but show varying nesting and hatching success rates. However, the pattern of re-nesting does not match the hatching success rates of nests in the study areas. Thus, the east-north-east zone had the greatest nesting success rate (65%) and hatching success rate (56%) in contrast with the east-south-east zone, which contains the beach with the lowest nesting success rate (22%) and hatching success rate (5.1%) of the whole island (Patino-Martinez et al., 2022a). Therefore, neither nesting success rate nor hatching success rate seems to be a reliable indicator of consistency in the choice of re-nesting beaches.

Some populations of loggerhead turtles prefer to nest in areas with greater wind and wave exposure and therefore such nesting occurs preferentially in areas with greater relative exposure index values (Garcon et al., 2010). Although it was not possible to record either wind velocity or wind direction in this study, the high-preference areas had taller waves during the nesting season, emphasizing the relationship between relative exposure index values and nesting distribution.

Access to currents enables loggerhead turtle neonates to escape rapidly from predator-rich coastal areas (Putman et al., 2010; Scott et al., 2014a,b). This means potentially that exposed beaches are of greater value for nesting.

Intra-beach nest site selection

At the intra-beach microhabitat level, female loggerhead turtles did not show a pattern of random re-nesting but rather a tendency to re-nest in areas with a medium or low risk of flooding/tidal erosion. Only a small per cent of female loggerhead turtles re-nested in areas with a high risk of flooding and erosion. Significant consistency in nest site selection at the backs of beaches has been observed for other sea turtle species (Hays et al., 1995; Kamel & Mrosovsky, 2004, 2006; Patrício et al., 2018). This behaviour could be driven by environmental factors (e.g. sea turtles could detect whether sand humidity is below the necessary threshold or whether the beach slope ensures adequate nest elevation; Patrício et al., 2018). The location of the next nest of females that previously nested in an area of high flood risk is more likely to be in lower-risk areas. There are potential advantages of nesting in different beach areas, such as the variability of hatchling phenotypes that this type of nesting facilitates. Different temperature and water incubation regimes affect the size of hatchlings (Glen et al., 2003; Read et al., 2013), which leads to variability in predation rates, ultimately affecting fitness (Spencer, 2002; Wood et al., 2014). In addition, as sea turtles have temperature-dependent sex determination (Yntema & Mrosovsky, 1980; Chan & Liew, 1995; Chevalier et al., 1999; Godley et al., 2002), nests closer to the sea with lower incubation temperatures could produce more males despite the greater flood risk. Male sea turtle are of high conservation value in the context of anthropogenic global warming, which is leading to the feminization of several populations (Jensen et al., 2018).

Loggerhead turtles nesting on Maio Island are philopatric but appear to use a bet-edging strategy, distributing their nests amongst several beaches. This could decrease the risk of losing all their nests in any adverse event on a single beach. This strategy has adaptive potential for the colonization of new, optimal incubation areas in the face of gradual environmental changes. Simultaneously, the choice of safe areas within each beach maximizes reproductive success, thus producing a strategic combination for nest site selection.

Adaptation to global changes

Under future sea-level rise scenarios a net recession of coasts is expected, which will lead to a reduction in sea turtle nest survival (Fish et al., 2005; Varela et al., 2019). Although interest in the effects of climate change on sea turtles is increasing (Araujo & Rahbek, 2006; Hawkes et al., 2007; Hays et al., 2010; Fuentes et al., 2011; Dalleau et al., 2012; Abella Perez et al., 2016; Laloë et al., 2017; Patrício et al., 2019), the potential for sea turtles to adapt to this environmental change remains to be investigated. One adaptive strategy could consist of turtles colonizing new suitable areas where sea-level rise or increased temperatures will have less impact. On oceanic islands such as Maio Island this mechanism is limited by the lack of shoreline continuity.

This study provides detailed information on sea turtle renesting behaviour in relation to philopatry to nesting areas and at the intra-beach microhabitat level, allowing us to predict potential future responses of sea turtles to sea-level rise. Extreme fidelity to nesting beaches was not observed, which will increase the probability of finding favourable environmental conditions for incubation. However, individual consistency in the selection of areas with medium or low flood risk would facilitate greater reproductive success (Garmestani et al., 2000; Patrício et al., 2018). How these traits will respond to sea-level rise is unknown and, in addition, natural physical factors can influence trends of shoreline erosion and accretion, and anthropogenic factors such as development could influence erosion trends and sea turtle behaviour (Patino-Martinez et al., 2017; Armstrong & Lazarus, 2019; Patrício et al., 2019; Lyons et al., 2020; Veelenturf et al., 2020).

Conservation importance

The data from this study could shape decisions on habitat management and help define future conservation plans for sea turtle nesting habitats. The entirety of Maio Island provides suitable nesting sites for loggerhead turtles and hosts a globally significant, large number of nests (Patino-Martinez et al., 2022a,b), but the east coast Island is a preferred loggerhead turtle nesting area. The inter-annual spatial distribution of sea turtle nests is often similar across different species and regions (Wheelwright & Mauck, 1998; Weishampel et al., 2003). Therefore, in view of existing urban development and tourism plans, we recommend that the entire eastern part of Maio Island should be considered a high-priority area for conservation. We recommend that current conditions on these nesting beaches should be preserved and protected against human settlements, modification and lighting.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, and did not involve human subjects, experimentation with animals and/or collection of specimens.

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