

Joana Filipa Silva Revés

**Nesting Biology of Green Sea Turtles (*Chelonia mydas*), in
Príncipe Island, Gulf of Guinea, Central Africa**



UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

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**Nesting Biology of Green Sea Turtles (*Chelonia mydas*), in
Príncipe Island, Gulf of Guinea, Central Africa**

Mestrado em Biologia Marinha

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À memória de Paulo Anunciada,

tio e amigo.

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Abstract

The green turtle (*Chelonia mydas*) hosts major nesting colonies in the Atlantic including São Tomé and Príncipe, where green sea turtles are the most common turtle species and Príncipe Island serves as a key nesting location. This rookery is known for exhibiting high genetic diversity, being an important genetic pool for the region. This study evaluated trends in the green turtle nesting population of Príncipe Island using data collected by Fundação Príncipe from 2015/16 until 2022/23 and data already published for Praia Grande from 2007/08 to 2014/15. Monitoring of sea turtle nesting activities occurs on all 36 nesting beaches from 1st September until the 30th of April and is divided into night and morning patrols during adult female and hatchling emergence. Green turtles followed a temporal distribution pattern that aligned with one of the dry periods (*Gravaninha*) and coincided with the nesting of São Tomé (August – March). Peaking between December and January, green turtles showed a preference for the eastern side of the island and a strong site fidelity. However, movements between nearby beaches were observed. Praia Grande and Praia Infante were the favourite nesting beaches, possessing ~ 80% of all nesting activity. 11,847 nests were monitored, with no significant increase in the nesting population, however, Praia Grande revealed consistent growth in nesting activity over 16 consecutive seasons, with a clutch frequency of 3.3 ± 1.8 clutches/season (range: 1-9). An estimated 884 nesting green turtle individuals was determined for the last three seasons, which revealed to be six times more than from the nesting seasons of 2007/08 – 2009/10. Long-term data analysis is still in need for determining definitive trends. Mean curved carapace lengths (99.4 ± 5.8 cm) of nesting females were smaller compared to other Atlantic populations, and similar to São Tomé. Clutch size (111 ± 22 eggs/clutch) also proved to be slightly lower from near green turtle populations and similar to São Tomé island's average, likely due to the smaller size of nesting females. Hatching success was relatively high ($88.9 \pm 5.2\%$), but overestimations might have happened, since important data was missing like the percentage of 'lost nests' of the island, and detailed information of predation numbers. Predation was primarily made by dogs and tufted ghost crabs, remaining a significant threat to nesting success.

Keywords: Sea turtles; *Chelonia mydas*; nesting trends; temporal distribution; predation; hatching success

Resumo

Para uma conservação eficaz de espécies vulneráveis, como as tartarugas marinhas, é necessário compreender o estado da sua população e as suas ligações ambientais, prevendo a sua viabilidade. Pressões sobre estas espécies conduziram a declínios significativos das populações ao longo dos séculos e, apesar dos progressos na investigação e conservação destas espécies ocorridos nas últimas décadas, muitos aspetos da sua biologia permanecem desconhecidos, continuando as suas populações a diminuir.

A tartaruga-verde (*Chelonia mydas*) está atualmente classificada como ameaçada pela Lista Vermelha da IUCN devido à degradação do seu habitat e exploração das suas áreas de alimentação e descanso. Apesar de possuírem uma população global de mais de 2 milhões de indivíduos, o seu ciclo de vida complexo, caracterizado por um atraso na maturidade sexual e migrações de longa distância, tornam-nas vulneráveis a fatores ambientais e antropogénicos, como a poluição, alterações climáticas e caça furtiva.

No Oceano Atlântico, uma das principais colónias de nidificação situa-se em São Tomé e Príncipe. Situada no Golfo da Guiné, acolhendo populações importantes de tartarugas marinhas, estudos anteriores mostraram que a colónia de tartarugas verdes de São Tomé e Príncipe apresenta uma elevada diversidade genética quando comparada com os valores registados noutras colónias atlânticas, sendo especialmente elevada quando confrontada com outras populações do Atlântico Oriental, constituindo um importante reservatório genético para a região. Pertencente ao arquipélago de São Tomé e Príncipe, na ilha do Príncipe, esta é a espécie mais abundante, nidificando em praticamente todas as praias arenosas da ilha. Embora existam desafios, estão em curso, na Ilha do Príncipe, esforços para melhorar a conservação e a compreensão da ecologia e da distribuição das tartarugas marinhas, como é o caso da implementação de Áreas Marinhas Protegidas (AMPs) e legislação local. No entanto, existem ainda lacunas significativas na compreensão da ecologia e biologia das tartarugas verdes desta região.

Neste estudo, foram avaliadas tendências de nidificação, distribuições temporal e espacial, sucesso da eclosão e risco de predação dos ninhos, bem como a biometria das fêmeas nidificantes. Através da análise de dados de campo de longo prazo foi possível compreender o impacto dos fatores ambientais e das ações de conservação no sucesso reprodutivo. Em última análise, o

objetivo era oferecer recomendações para melhorar a conservação e a gestão das tartarugas marinhas verdes do Príncipe.

Este estudo foi realizado na Ilha do Príncipe, onde, desde 2015, a Fundação Príncipe assume a responsabilidade da monitorização de todas as praias nidificantes. Esta tese utilizou dados recolhidos a partir de 2015/16 para toda a análise, assim como dados de abundância fornecidos e já publicados para a Praia Grande de 2007/08 a 2014/15 por Loureiro et al. (2011) (2007/08 - 2009/10) e Ferreira et al. (2019) (2007/08 - 2015/16).

A monitorização das atividades de nidificação é realizada anualmente em todas as 36 praias de nidificação da ilha, de 1 de setembro a 30 de abril. Esta divide-se, numa primeira fase, em patrulhas noturnas (por terra) e matinais (por mar), durante a emergência das fêmeas adultas (de 1 de setembro até final de fevereiro), e, numa segunda fase, durante a emergência dos recém-nascidos (de 1 de março a 30 de abril).

Patrulhas noturnas são realizadas todos os dias entre as 18h00 e as 05h00 nas praias acessíveis por terra; e as patrulhas matinais, destinadas a praias inacessíveis a pé, realizadas por barco, das 08h00 às 14h00, alternando entre praias do norte e do sul, todos os dias. Estes relatórios são realizados para avaliar a ocorrência e distribuição das atividades de nidificação, medir as fêmeas nidificantes, registar evidências de predação dos ninhos e monitorizar o sucesso da eclosão e emergência dos recém-nascidos. Durante os levantamentos, toda a praia é examinada e todas as emergências de tartarugas marinhas são registadas e classificadas como: 1. ninho bem-sucedido, 2. tentativa de ninho, ou 3. falsas rastejantes (ou meia-lua). Todos os ninhos encontrados são marcados com uma estaca de madeira numerada até ao dia da sua exumação. O processo de exumação (escavação do ninho) decorre durante o dia, das 08h00 às 15h00.

Neste estudo, a população de tartarugas verdes do Príncipe seguiu um padrão de distribuição temporal que se alinhou com um dos períodos secos da ilha (*Gravaninha*) e que coincidiu com a época de desova da população de São Tomé (agosto - março). Com um pico entre dezembro e janeiro, as tartarugas-verdes mostraram uma preferência pelo lado oriental da ilha e uma forte fidelidade ao local, regressando às mesmas praias de nidificação de forma consistente. No entanto, foram observados movimentos entre praias próximas o que realça a necessidade de uma marcação e monitorização mais abrangentes. A Praia Grande e a Praia Infante demonstraram esta fidelidade, sendo as praias preferidas para nidificação e possuindo quase 80% de toda a atividade de desova

observada. Porém, com o tempo, as alterações climáticas poderão ter impacto nos padrões de nidificação devido a mudanças na precipitação e nas características das praias, o que poderá influenciar a distribuição futura dos locais de desova, com as tartarugas a favorecerem possivelmente praias com melhores condições ambientais.

Durante oito anos consecutivos foram observados 11.847 ninhos na ilha do Príncipe com flutuações anuais consideráveis, mas não foi visualizado um aumento significativo na tendência de nidificação, devido ao seu pequeno período de monitorização. Ainda assim, a Praia Grande, considerada como a praia índice deste estudo, revelou um crescimento significativo na atividade de desova ao longo de 16 épocas de nidificação consecutivas, com uma frequência de ninhos de $3,3 \pm 1,8$ ninhos/época (intervalo: 1-9) colocados por cada fêmea nidificante. Não é ainda possível determinar se isso será um reflexo do crescimento real da população ou se poderá estar ligado aos maiores esforços de pesquisa desde a monitorização padronizada pela Fundação Príncipe.

Relativamente à ilha do Príncipe, foi obtida uma estimativa de 884 tartarugas verdes nidificantes nas últimas três épocas, o que revelou um crescimento de população seis a sete vezes mais do que nas épocas de nidificação de 2007/08 - 2009/10. A análise de dados a longo prazo continua a ser necessária para determinar tendências definitivas.

A população nidificante do Príncipe apresentou comprimentos médios da carapaça curvada ($99,4 \pm 5,8$ cm) mais pequenos em comparação com outras populações atlânticas, mas semelhantes às fêmeas nidificantes de São Tomé. O tamanho da desova (111 ± 22 ovos/ ninhada) também se revelou ligeiramente inferior ao das populações de tartarugas verdes mais próximas e semelhante à média da ilha de São Tomé, provavelmente devido ao tamanho inferior das fêmeas.

O sucesso de eclosão foi relativamente elevado ($88,9 \pm 5,2\%$) quando comparado com outras populações, o que poderá indicar condições de nidificação favoráveis. Poderão ter sido feitas sobrestimações, uma vez que faltaram dados importantes como a percentagem de 'ninhos perdidos' na ilha e informação detalhada sobre o número de predadores. As taxas médias de sucesso de eclosão foram também determinadas para a Praia Grande, onde foi possível obter números dos 'ninhos perdidos' de cada temporada ($58,4 \pm 21,9\%$ com 'ninhos perdidos' e $89,8 \pm 20,9\%$ sem 'ninhos perdidos'), o que reflete uma redução considerável no sucesso global.

Com uma variedade de predadores, a predação foi feita principalmente por cães e caranguejos-fantasma, permanecendo uma ameaça significativa para o sucesso da nidificação.

Este estudo foi a primeira descrição da população de tartarugas marinhas verdes da Ilha do Príncipe, realçando a importância de esforços contínuos de conservação e monitorização detalhada, assim como da abordagem dos desafios ambientais.

Palavras-chave: Tartarugas marinhas; *Chelonia mydas*; tendências de nidificação; distribuição temporal; sucesso de eclosão

Table of contents

Acknowledgements	iv
Abstract	vi
Resumo	vii
Table of contents	xi
List of figures	xiii
List of tables	xiv
1. Introduction	1
2. Methodology	4
2.1. Study area	4
2.2. Beach surveys and data collection	6
2.3. Nesting Abundance.....	9
2.3.1. <i>Nesting Abundance of Príncipe Island</i>	9
2.3.2. <i>Nesting abundance and population estimate of Praia Grande</i>	9
2.4. Nesting female biometry and clutch size	10
2.5. Hatching success.....	11
2.5.1. <i>Hatching success in Praia Grande</i>	11
2.6. Clutch predation.....	12
2.7. Data Analysis.....	12
3. Results	13
3.1. Temporal distribution of green sea turtles' nests.....	13
3.2. Spatial distribution of green sea turtles' nests	14
3.3. Nesting abundance trends for the island and for Praia Grande	17
3.4. Nesting female biometry and clutch size	21

3.5. Hatching Success	22
3.6. Clutch predation	24
4. Discussion.....	26
4.4. Temporal and spatial distribution:	27
4.2. Nesting Abundance and trends	29
4.3. Nesting female biometry and clutch size.....	31
4.4. Hatching success.....	32
4.5. Clutch predation.....	33
3.6. Suggestions for the future.....	35
5. Conclusions	35
6. Appendix	37
7. References	38

List of figures

Figure 1: (a) Map of São Tomé and Príncipe archipelago and location of Príncipe Island; (b) Map of Príncipe Island (1° 36' 59.99" N; 7° 23' 59.99" E); (c) Location of São Tomé and Príncipe archipelago in the Gulf of Guinea, Central Africa.	5
Figure 2: Mean temporal distribution of green sea turtles' nests at Príncipe Island, by 14 day-intervals during eight consecutive nesting seasons (2015/16 to 2022/23).	14
Figure 3: Location of the 36 beaches (portrayed by green dots) in Príncipe Island monitored for sea turtle nesting activities, and their respective mean percentage of green sea turtles' nests, across eight nesting seasons, from 2015/16 to 2022/23. Beaches not named in the picture represent a nesting percentage of around zero.	15
Figure 4: Number of green sea turtles' nests around Príncipe Island, from 2015/16 to 2022/23 nesting seasons.	17
Figure 5: Spatial distribution of green sea turtles' nests during different nesting seasons (2015/16 – 2022/23) in Príncipe Island. The graphs represent the absolute number of nests in each beach, and each season exhibits the six beaches with the highest number of nests in that year.	18
Figure 6: Number of green sea turtles' nests in Praia Grande, at Príncipe Island, during 16 consecutive nesting seasons: from 2007/08 to 2022/23. $r^2 = 0.51$, $p\text{-value} = 0.0018$	19
Figure 7: Observed clutch frequency of the nesting green sea turtles in Praia Grande, Príncipe Island.	20
Figure 8: Curved carapace length (CCL) distribution of green sea turtle nesting females ($n = 4422$) from Príncipe Island, through the seasons of 2015/16 to 2022/23.	21
Figure 9: Correlation between curved carapace length (CCL) and clutch size (Number of eggs per clutch) in green turtles from Príncipe Island, Central Africa ($n = 4422$ nesting females). $r^2 = 0.0039$, $p\text{-value} < 0.001$	22
Figure A1: Green turtle hatching success per nesting season in Príncipe Island. The top panel corresponds to estimates of H% without the 'lost nests'; the bottom panel represents the hatching success including 'lost nests' with H% = 0. Mean values are marked with an 'X'. The box the hatching success range and dots represent outliers.	37

List of tables

Table 1: Monitored beaches of Príncipe Island for sea turtle nesting activities and their respective length and location.	8
Table 2: Monitored beaches of Príncipe Island for sea turtle nesting activities and their respective length and number of nests (expected and observed).	16
Table 3: Hatching success (H%) (\pm SD) of green turtle clutches at all nesting beaches of Príncipe Island (including Praia Grande), and only at Praia Grande. In Praia Grande, hatching success was estimated both excluding ‘lost nests’ and including these with H%=0. These estimates represent only the hatching success associated with abiotic factors, ignoring clutch predation.	23
Table 4: Clutch predation of green sea turtle’s nests between 2015/16 to 2022/23, from all nesting beaches of Príncipe Island, in absolute values (n) with the respective average (\pm SD) and correspondent percentage. Proportion of predated nests = total predated nests/total exhumed nests.	24
Table 5: Clutch predation of green sea turtle’s nests from 2015/16 to 2022/23 at Praia Grande (index beach) of Príncipe Island in absolute values (n) with the respective average (\pm SD) and correspondent percentage. Proportion of predated nests = total predated nests/total exhumed nests.	26

1. Introduction

The effective conservation among vulnerable species like sea turtles starts with the understanding of their population status, through the process of viability predictions and recognition of their environmental connections (Ceriani et al., 2019; Wyneken et al., 2013). They are a vital part of marine ecosystems, ensuring the health of seagrass beds, coral reefs, and biodiversity (Lutz & Musick, 1997). Nevertheless, due to habitat destruction, pollution, climate change, and poaching, all seven species of sea turtles are threatened or endangered globally (IUCN, 2021) at present. These pressures have resulted in significant population declines over the centuries, with their migratory nature and reliance on numerous habitats making them all the more vulnerable (Catry et al., 2009a; Troëng & Chaloupka, 2007) and their migratory nature and reliance on various habitats make them especially vulnerable (Lutz & Musick, 1997; Seminoff et al., 2015). Environmental stressors like rising water temperatures, pollution, and marine toxins weaken their immune systems further, making them even more susceptible to a variety of pathogens (Chaloupka, Kamezaki, et al., 2008). Sea turtles may be used as indicators of ecosystem health, and diseases like fibropapillomatosis can be helpful in the monitoring of near-shore habitats (Lutz et al., 2003; Lutz & Musick, 1997). Although this has resulted in certain conservation success stories in recent decades (Chaloupka, Bjorndal, et al., 2008), a great deal of sea turtle biology remains unknown, and populations continue to decline. This is the case with developing nations in particular, where limited data and few conservation efforts have been recorded (Eckert et al., 1999). Specific cases include parts of Africa that are home to important nesting and feeding grounds.

The green turtle (*Chelonia mydas*), currently listed as Endangered by International Union for the Conservation of Nature's Red List of Threatened Species (Seminoff et al., 2015), has a global population exceeding 2 million individuals (Broderick et al., 2001; Chaloupka, Bjorndal, et al., 2008). Due the high range of habitats they are exposed to, e.g. coastal nesting areas, epipelagic habitat, neritic foraging grounds, and coastal and oceanic migratory pathways (Balazs, 1976; Luschi et al., 2003), these biological characteristics expose green turtles to a variety of anthropogenic impacts, and as such, there has been a substantial decline at a global scale of this species (Lewison et al., 2014; Wallace et al., 2013).

Green turtles are large marine turtles with a global distribution across tropical and subtropical waters (Chaloupka & Limpus, 2001). They nest on sandy beaches and are herbivorous

or omnivorous as adults, feeding mainly on algae and seagrasses, and also invertebrates (Lutz & Musick, 1997). These turtles undertake extensive migrations, sometimes spanning thousands of kilometres, between breeding and foraging grounds (Hirth, 1980; Lutz & Musick, 1997). Their life cycle is complex, characterized by delayed sexual maturity (Miller, 1997) and long-distance migrations, requiring large energy reserves for reproductive travel (Broderick et al., 2001). These migrations are highly dependent on environmental conditions at their foraging grounds. Breeding adults show strong natal homing behaviour, returning to their birthplace to nest, and display fidelity to specific nesting sites (Meylan et al., 1990). Female green turtles return to nest every 2-5 years after feeding extensively to accumulate energy (Seminoff et al., 2015). Once at the nesting site, they lay multiple clutches of eggs over a period of 10-14 days, producing 2-6 clutches per season, depending on environmental conditions and individual health (Bowen & Karl, 2007; Hays & Scott, 2013). Molecular evidence reveals a significant split between green turtle populations from the Atlantic-Mediterranean and Indo-Pacific regions (Bowen et al., 1992; Bowen & Karl, 2007; Seminoff et al., 2015). Even within the Atlantic-Mediterranean, populations exhibit strong genetic structuring, suggesting a tendency for female natal philopatry (Nishizawa et al., 2011). As a result, each nesting colony should be treated as a separate conservation unit. In the Atlantic, major nesting colonies include Tortuguero, Costa Rica (Bjorndal & Carr, 1989); Ascension Island, UK (Mortimer & Carr, 1987); Suriname (Schulz, 1975); Aves Island, Venezuela (Sole and Medina, 1989); Poilao, Guinea Bissau (Catry et al., 2009b); and Trindade, Brazil (Almeida et al., 2011). In the Eastern Atlantic, Guinea-Bissau hosts the largest known rookery, with over 25,000 nests laid annually (A. R. Patrício et al., 2019), followed by São Tomé and Príncipe (330 to 3,200 nests annually, Ferreira-Airaud et al., 2022) and Bioko (170 to 1,830 nests, Honarvar et al., 2016).

Green turtle populations along the Atlantic coast of Africa face numerous threats, including heavy exploitation for meat and eggs (Weir et al., 2007). Habitat degradation due to coastal development, sand mining, pollution, and oil drilling also pose significant risks (Formia et al., 2006). Given their long generation times and migratory nature, green turtles are vulnerable across large geographic ranges, meaning threats to one habitat, like nesting grounds, may be exacerbated by dangers in other parts of their range, such as unprotected migration routes (Meylan et al., 2011).

In São Tomé and Príncipe, green sea turtles are the most common turtle species, with Príncipe Island serving as a key nesting location (Castroviejo et al., 1994; Ferreira-Airaud et al.,

2022b). These turtles use virtually all sandy beaches on the island, which offers suitable nesting sites along its diverse coastline (Ferreira et al., 2019; Ferreira-Airaud et al., 2022b; Loureiro et al., 2011). The green turtle population on Príncipe is genetically distinctive and plays an important role in the marine biodiversity of the Gulf of Guinea, representing an important genetic pool in the region (Formia et al., 2006; Hancock, 2019). Príncipe Island belongs to the archipelago of São Tomé and Príncipe, situated in the Gulf of Guinea. The Gulf of Guinea harbours major nesting aggregations of sea turtles, as well as regionally important populations of green turtles (Formia et al., 2006). Findings of Formia et al. (2006), who based solely on mtDNA data, showed that São Tomé and Príncipe's rookery exhibits high genetic diversity when compared with values reported for other Atlantic rookeries and being especially high when compared to other Eastern Atlantic populations. Efforts to improve the conservation and understanding of sea turtle ecology and distribution in São Tomé and Príncipe are ongoing, but challenges remain in securing long-term sustainability and protection.

Príncipe was designated a UNESCO World Network of Biosphere Reserve in 2012 due to its unique biodiversity and ecosystems (Ceríaco et al., 2021; Ferreira-Airaud et al., 2022b). The island features rich biodiversity, including numerous endemic terrestrial and marine species (Ceríaco et al., 2021). Conservation efforts on Príncipe include Marine Protected Areas (MPAs) and regional laws, with local authorities prioritizing sustainable development to avoid harmful activities like coastal development and pollution that could threaten species such as sea turtles. One of the primary organizations spearheading sea turtle conservation is Fundação Príncipe (FP), which emphasizes the participation and engagement of local communities as essential for successful conservation (Ferreira-Airaud et al., 2022a). Despite the introduction of a national law in 2014 that criminalizes the exploitation of sea turtles and their by-products (Decreto-Lei nº8/2014), enforcement and community involvement remain challenges in improving sea turtle conservation. The remote beaches of Príncipe Island provide relatively undisturbed and favourable conditions for nesting, while its surrounding waters offer ample feeding grounds for both juveniles and adults (Castroviejo et al., 1994; R. L. Ferreira et al., 2018; Ferreira-Airaud et al., 2022b). The island's low levels of human activity and minimal coastal development reduce many of the typical threats faced by sea turtles globally, such as light pollution and beach erosion. However, the illegal capture both at sea, by illegal fisheries, and on land in non-monitored beaches play a decisive role for the well develop of the vulnerable species on the island. Natural predators like crabs and birds, along

with occasional poaching, pose, as well, threats to eggs and hatchlings. Conservation efforts on Príncipe focus on protecting nesting females and their eggs, which directly benefit the local community by supporting ecotourism and maintaining the island's rich marine biodiversity. Despite increasing conservation efforts on Príncipe, much of the island's sea turtle ecology remains poorly understood. Key aspects such as the migratory routes of green turtles, population dynamics, and long-term survival rates are still largely unknown. Additionally, the potential impacts of climate change—such as rising sand temperatures affecting hatchling sex ratios—have not been fully studied. Addressing these gaps in knowledge is critical for developing conservation strategies tailored to Príncipe's unique environment. Furthermore, while São Tomé and Príncipe are recognized as key nesting sites for sea turtles there is still a lack of comprehensive understanding of the region's green turtle populations. Limited data on their biology, spatial and temporal distributions of nesting activities, hatching success and predation risk, and biometry of nesting females. Most research on Príncipe has focused on a small portion of the island's beaches, leaving the full extent of nesting activity unknown.

This study aims to evaluate trends in the green turtle nesting population on Príncipe Island investigating the nesting patterns, hatching success, and potential threats to incubating clutches. Through the analysis of long-term field data, it will provide insights into how environmental factors and conservation actions impact reproductive success. Ultimately, the goal is to offer data-driven recommendations for improving the conservation and management of green sea turtles on Príncipe, ensuring their long-term survival among growing environmental challenges. The study also aims to assess the population trends and nesting activity changes over recent years, providing crucial information on nesting abundance, distribution, and on the number of breeding females on the island.

2. Methodology

2.1. Study area

The present study was conducted on Príncipe Island (1° 36' 59.99" N; 7° 23' 59.99" E), located in the Gulf of Guinea, Central Africa, approximately 220 km west of the African continent

(Costa Alegre, 2009) (Figure 1). It is the smaller and northern of the two major islands in the São Tomé and Príncipe archipelago, covering 142 km² (Plano Diretor Da Região Autónoma Do Príncipe, 2018) and separated by 145 km to the northeast of São Tomé, and 205 km southwest of Bioko. Surrounded by various inhabited islets, Príncipe is the oldest island in the Gulf of Guinea, formed by volcanic activity around 30 million years ago, originated from the Cameroon Line. The island is characterized by rugged terrain, with volcanic peaks, dense rainforests, and sandy beaches. Its highest point is Pico Príncipe, which rises to about 942 meters above sea level.

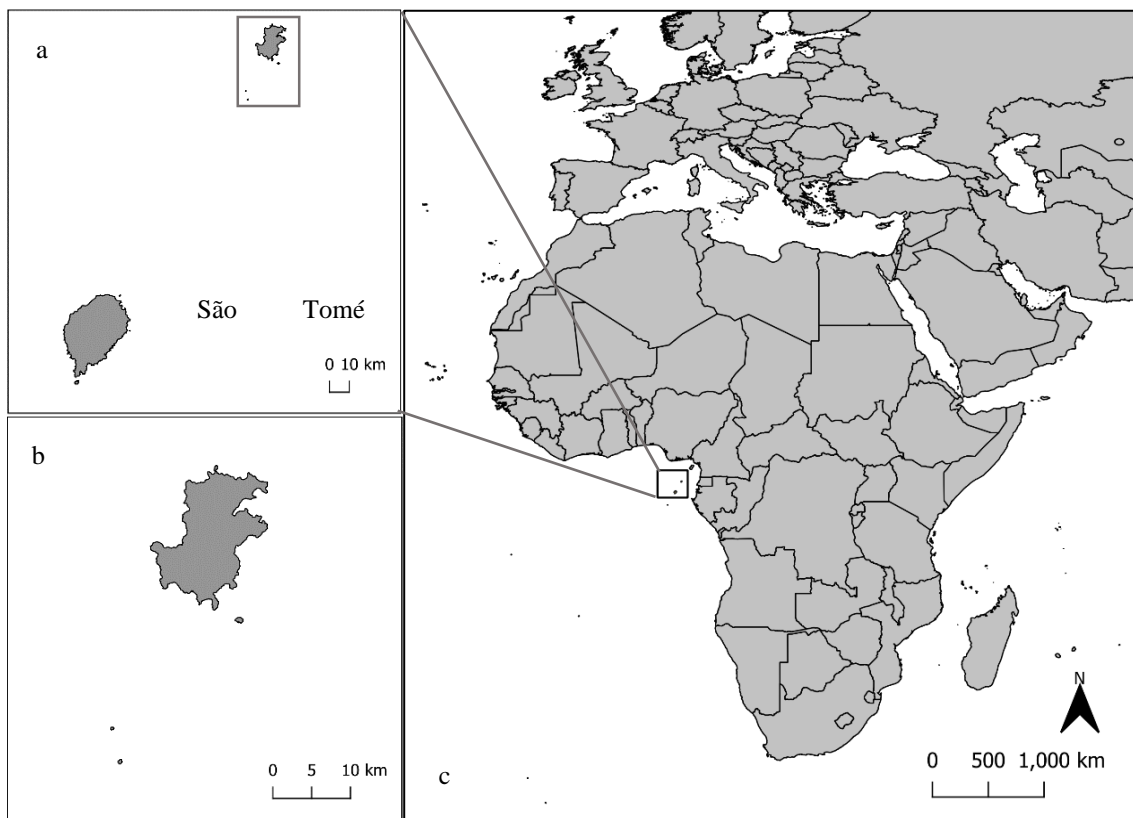


Figure 1: (a) Map of São Tomé and Príncipe archipelago and location of Príncipe Island; (b) Map of Príncipe Island (1° 36' 59.99" N; 7° 23' 59.99" E); (c) Location of São Tomé and Príncipe archipelago in the Gulf of Guinea, Central Africa.

Príncipe has a warm and humid equatorial climate, with mean temperatures above 25 °C at sea level. There are two dry seasons in Príncipe, which are determined by the Intertropical

Convergence Zone: the *Gravana* (June to mid-September) and the *Gravanita/Gravaninha* (a few weeks between mid-December and March). The rest of the year experiences high rainfall, supporting the dense vegetation. The second drier season is characterized by higher temperatures and lower precipitation levels and largely overlaps with the reported sea turtle nesting season (Graff, 1996).

Príncipe features a variety of coastal habitats, such as rocky reefs, seagrass meadows, estuaries, mangroves, and both sandy and rock coastlines. Beaches vary considerably in sand colour, with black to white sand, abundant flora dominated by coconut palms and beach almond trees, as well as lower vegetation and dried coconut shells. Northern shores hold a larger shallow shelf and little wave exposure, whereas the southern coast has shorter and deeper shores that are more wave prone. Most of the southern beaches are especially isolated, with practically no human settlements (Ferreira-Airaud et al., 2022a), which distinguishes them from the shorelines in the northern part of the Island where the majority of the population inhabits. Clear warm waters with rocky reefs and seagrass meadows create ideal conditions for marine species. The archipelago's shallow coastal shelf (less than 200 m wide) has been recently depicted as holding relatively important aggregations of foraging juvenile green turtles in the Gulf of Guinea (Hancock, 2019).

2.2. Beach surveys and data collection

Monitoring of sea turtle nesting activities in São Tomé and Príncipe started in 2002 by the NGO MARAPA (Sea Environmental and Traditional Fisheries) and in 2009 'Programa SADA' followed, managed by the University of Algarve, Portugal, under an agreement with the Regional Government of Príncipe. Lastly, Fundação Príncipe (FP) took accountability since 2015 until the present year (2023), with the introduction of beach surveys on all nesting beaches of Príncipe Island and the implementation of a more constant and thorough monitorization. This study used data collected by Fundação Príncipe from 2015/16 until the 2022/23 nesting season, for all the analysis, and abundance data provided and already published for Praia Grande from 2007/08 to 2014/15 by Loureiro et al. (2011) (2007/08 – 2009/10) and Ferreira et al. (2019) (2007/08 – 2015/16), being complemented by new information.

Monitoring of sea turtle nesting activities is conducted annually on all 36 nesting beaches of Príncipe Island (Table 1) from 1st September until the 30th of April, since 2015/16. During July

and August, rare nests appear which are also reported to FP. In Praia Grande, beach patrols have been conducted annually since 2002, but only nesting records from 2007/08 and above are available. This beach serves as an index beach for this study, for sea turtle monitoring activities, being the main nesting beach in the island. Thus, we assume that the yearly abundance patterns of green sea turtles in Praia Grande, are representative of a larger pattern that occurs at all other beaches in Príncipe, used by the same nesting population.

Annually, data collection is divided into night (by land) and morning patrols (by land and sea) during adult female emergence (from 1st September until end of February), and day monitoring during hatchling emergence (from 1st of March until 30th of April). During the peak nesting activity, night patrols are conducted every day between 18h00 and 05h00 at Praia Boi, Praia Bumbo, Praia Grande, Praia Infante, Praia Ponta Marmita, Praia Micotó, Praia Montanha, and Praia Sundy (Table 1) all of which are beaches accessible by land. Morning patrols (or marine surveys) are conducted by boat, alternating between north (Table 1) and south beaches (Table 1) each day, from 08h00 until 14h00, counting turtle tracks from the previous night. Marine surveys are aimed at inaccessible beaches on foot. The night patrol's team consists of two beach patrollers on each beach and the marine team involves four members every day. These surveys are carried out to assess the occurrence and distribution of green sea turtle nesting activities, measure nesting females, record evidences of clutch predation, and monitor hatching success and hatchling emergence.

During the surveys, the whole beach is examined, and all the sea turtle emergences are recorded and classified as: *successful nest*, resulting in oviposition; *nesting attempt*, where turtles dig one or various nests, but return to the sea without laying any eggs; and *false crawls (or half-moon)*, where females emerge to the beach, wandering and returning to the sea without a nest attempted. All nests found are marked with a numbered wooden stake until the day of its exhumation. Exhumation process (nest excavation) takes place during daytime, from 08h00 until 15h00, every day, and it was performed by two patrollers.

Table 1: Monitored beaches of Príncipe Island for sea turtle nesting activities and their respective length and location.

Beach	Length (m)	Location	Period of Monitoring	Lat	Long
Praia Areia	260	South	Day	1.640568	7.442860
Praia Banana	200	North	Day	1.690314	7.441887
Praia Boi	320	North	Night	1.680611	7.459740
Praia Bombom	680	North	Day	1.690697	7.400110
Praia Bumbo	800	South	Night	1.603786	7.425301
Praia Burra	760	North	Day	1.684005	7.435034
Praia Cabinda	400	South	Day	1.563198	7.421949
Praia Caixão	270	West	Day	1.630947	7.367805
Praia Cajú	180	North	Day	1.689703	7.439966
Praia Campanha	440	North	Day	1.683856	7.426694
Praia Cemitério	210	South	Day	1.571087	7.426042
Praia Esprinha	290	West	Day	1.631282	7.456731
Praia Franguinha	110	North	Day	1.687464	7.419172
Praia Grande	1400	North	Night	1.672106	7.447838
Praia Infante	1400	South	Night	1.557734	7.416946
Praia Lapa	620	West	Day	1.619014	7.369372
Praia Macaco	500	North	Day	1.681904	7.453217
Praia Margarida	90	North	Day	1.681157	7.373778
Praia Maria Correia	455	West	Day	1.606353	7.364411
Praia Ponta Marmita	50	North	Night	1.682970	7.371685
Praia Micotó	500	North	Night	1.679983	7.384230
Praia Montanha	450	North	Night	1.681267	7.389479
Praia Novo	90	West	Day	1.688673	7.411994
Praia Pedra Furada	210	West	Day	1.660541	7.367957
Praia Pedrona	180	North	Day	1.687641	7.439741
Praia Ponta Ramiro	70	North	Day	1.679967	7.375165
Praia Popa	150	North	Day	1.685936	7.429141
Praia Portinho	470	South	Day	1.637777	7.446771
Praia Prainha	50	South	Day	1.630794	7.458716
Praia Ribeira Izé	580	North	Day	1.686593	7.395954
Praia Rio São Tomé	535	South	Day	1.559507	7.354489
Praia Santa Rita	620	North	Day	1.69096	7.405389
Praia Seca	450	South	Day	1.54588	7.399357
Praia Sundy	520	North	Night	1.679534	7.382002
Praia Uva	50	North	Day	1.674439	7.458704
Praia Yola	520	West	Day	1.648129	7.372534
Total	14880				

2.3. Nesting Abundance

2.3.1. Nesting Abundance of Príncipe Island

To estimate the total number of nests laid by breeding green sea turtles in Príncipe and their respective distribution across the nesting beaches, this study relied on the counts of *successful nests* marked in all 36 nesting beaches of the island. The actual number of clutches counted during surveys from 2015/16 to 2022/23 was used to determine the temporal and spatial distribution, and their corresponding abundance trends. For visual observation of the temporal distribution, the number of nests were pooled into 14-day intervals, which were divided by the total number of nests of each respective season, to obtain the nesting proportion across time. Then, an average was calculated for the eight consecutive nesting seasons. A mean of the clutches recorded for each beach, from 2015/16 to 2022/23 was used to exhibit their spatial distribution around Príncipe Island.

2.3.2. Nesting abundance and population estimate of Praia Grande

Praia Grande, as our index beach, illustrates the highest nesting activity in Príncipe, and the site for which more data is available, with abundance data collected since 2007/08 until 2022/23, representing 16 consecutive seasons of nesting evidence. Although this long period of data collection, monitoring was only standardized by FP after 2015/16, lacking some reports about data collection procedures in the previous years. Loureiro et al. (2011) described for the nesting seasons of 2007/08 until 2009/10 that night patrols were done by local unpaid associates non-continuously, meaning that there may be some inconsistencies in the surveys. (R. L. Ferreira et al., 2019) used body-pit counts to estimate the number of clutches, which differs from the methods by FP. From 2015/16 and forward, the actual number of green sea turtles' *successful nests* at Praia Grande were observed in real time during beach patrols. To assess any trend in population abundance, an average number of nests of the first (2007/08 – 2010/11) and last (2020/21 – 2022/23) three nesting seasons was obtained, since sea turtles do not usually undertake reproductive migrations every year, returning to nest every 3 to 5 years (Troëng & Chaloupka, 2007). For Príncipe, a mean remigration interval of 3 years was considered, in agreement with other South Atlantic green sea turtles' populations (e.g. Trindade Island, Brazil; Aves Island, Venezuela; Ascension Island, UK) (Seminoff et al., 2015).

Clutch frequency was estimated for green sea turtles nesting in Praia Grande. Through uniquely referenced flipper tags placed in both frontal flippers of all observed nesting females, and records of re-incident emergences, it was possible to obtain the mean clutch frequency for each nesting season from 2015/16 to 2022/23.

To estimate the population size of Príncipe, the number of annual nesting females in Praia Grande (*No of nests / Clutch frequency*) was multiplied by the remigration interval (*Remigration interval x No of nests / Clutch size*).

2.4. Nesting female biometry and clutch size

During oviposition, curved carapace length (CCL) was measured to the nearest mm, from the notch at the anterior of the carapace to the tip of the last posterior marginal scute using a flexible measuring tape. A wide range of different sized females was found, and an initial examination of the data allowed to detect some clear errors, with some values of CCL recorded that were impossibly small or large for nesting green turtles (e.g., records of turtles with 70 cm CCL or with 190 cm CCL). The CCL for nesting females of this species is widely reported to range between 72 cm, from Green Sea Turtles of the Mediterranean (Sönmez, 2019), and 143.5 cm, from turtles of the South Atlantic (Almeida et al., 2011). However, the Mediterranean population is known to have the smallest individuals. Thus, and in a very conservative way, records below 75 cm and above 150 cm were eliminated from this study data, being considered as measuring or record errors.

For clutch size, similar inaccurate values were found, with clutches ranging between 6 and 291 eggs, and the same elimination process was conducted where clutches below 40 (smallest “normal” clutch size for individual females) (Bjorndal & Carr, 1989) and above 180 eggs per clutch were removed from the calculations accordingly to Broderick et al. (2003), Hirth (1980) and Seminoff et al. (2015). Clutch size was calculated by the sum of *shells* and *unhatched eggs* found inside the nest. Due this initial filtering process, 109 nests were eliminated from the final data.

Additionally, predated nests were also excluded for the computation of clutch sizes, as these nests have an unknown number of eggs ‘stolen’/predated that was impossible to quantify.

2.5. Hatching success

To assess green sea turtle hatching success (H%) in Príncipe Island, data from exhumed nests of the 36 nesting beaches between the seasons 2015/16 and 2022/23 was used. Exhumation was performed after hatchling emergence and consisted in the excavation of the nests to count eggshells, number of alive and dead hatchlings, and unhatched eggs that were found inside the nest chamber. With this information, an estimation of the clutch size (*shells + unhatched eggs*) and hatching success ($shells / (shells + unhatched\ eggs) * 100$) were obtained for each exhumed nest.

A mean H% for each nesting season, for the whole island, was then calculated. Predation data was excluded from the analysis, since it can occur partially or totally, being unattainable to know the initial clutch size and, consequently, accurate H% values. Therefore, H% is considered the hatching success of green turtle clutches when predation does not occur. Predation will be analysed separately.

2.5.1. Hatching success in Praia Grande

Since 2015/16 exhumation was performed in all nesting beaches of Príncipe, but it was in Praia Grande where the biggest efforts were placed especially after hatchling emergence, mostly due to the inaccessibility and remote location of some nesting beaches.

At Praia Grande all nests are marked with wooden stakes uniquely numbered during night patrols and monitored thereafter. However, due to multiple reasons, the location of some nests is lost. This can be due to the removal of the stake by the action of the waves or by the nesting activity of another turtle, by large predators (e.g., dogs). However, it is important to clarify that ‘lost’ does not necessarily mean entire loss of the clutch nor a 0% hatching success rate. Some of these clutches may have been partially or totally flooded by the tide or destroyed by other turtles, while others might have remained intact, with the possibility of H% higher than zero (> 0%).

With all the nests with known location being monitored and excavated in Praia Grande, the number of ‘lost nests’ was possible to acknowledge, on this beach. These nests represent the difference between the number of initial marked nests and exhumed nests, translating to clutches for which the location was not possible to recover and, consequently, not excavated by the team.

The mean hatching success was thus determined in two different ways for Praia Grande. Firstly, excluding all ‘lost nests’, and secondly, including all ‘lost nests’ with an attributed hatching success value of zero. In both cases, predated clutches were excluded and were analysed separately. Estimates were obtained for 2015/16 to 2022/23 nesting seasons, were obtained, for both approaches.

2.6. Clutch predation

Clutch predation was estimated for all Príncipe Island nesting beaches and for Praia Grande alone, in agreement with the efforts placed into the excavation period, after hatchling emergence. Clutch predation was identified by predator species’ distinctive tracks, the presence of predated eggs around or inside the nest and evidence that the nest was excavated (e.g., by crabs, dogs, or others). If there were eggshells with signs of predation observed, they were counted and discarded to avoid double counting.

All monitored nests with known location, between the seasons 2015/16 to 2022/23, were observed for evidence of predation.

2.7. Data Analysis

A chi-square test for independence (χ^2) was used to address the spatial distribution of green sea turtles’ nests around Príncipe Island, to assess if turtles select their nesting sites randomly along the available nesting habitat or if, on the contrary, they have a preference for certain nesting beaches. For the chi-square test, the observed number of nests corresponded to the mean number of nests counted throughout the 8 nesting seasons (2015/16 to 2022/23) in each beach surveyed, while the expected number of nests per nesting beach was obtained by multiplying the total mean number of nests by the proportion of beach extension. Measurements for beach length analysis were obtained using Google Earth measuring tool program (Table 2). A map of the spatial distribution of the clutches was created in QGIS version 3.30.1 software using the mean nest percentage of each beach.

To analyse population trends over the years, correlation coefficients were calculated based on the number of nests recorded per nesting season for Príncipe Island and Praia Grande.

Additionally, a correlation analysis was performed to examine the relationship between the curved carapace length (CCL) of nesting females and their clutch size, testing the hypothesis that larger females tend to lay larger clutches.

A one-way ANOVA was run to compare hatching success (H%) across the nesting seasons (2015/16 – 2022/23), in all the island and in Praia Grande alone. For the later, a Wilcoxon test for paired samples was used to compare the differences between the two different methods used to calculate H% in Praia Grande (i.e., including and excluding ‘lost’ nests).

The percentage of clutch predation per year were estimated for Praia Grande and all the island, and then compared across nesting seasons (2015/16 – 2022/23) using a one-way ANOVA test.

All statistical analyses were performed using RStudio 2023.12.1 version and the Analysis ToolPak.

3. Results

3.1. Temporal distribution of green sea turtles’ nests

The temporal distribution of green turtle nests in all monitored nesting beaches was based on eight nesting seasons, between 2015/16 and 2022/23 (Figure 2). For Príncipe Island, the first nests tend to appear in the beginning of August (01/08 – 15/08) and the last ones are found around the end of March (13/03 – 26/03), with the nesting peak occurring during December and January (05/12 – 15/01), which represent 49.9% of all nests documented (Figure 2).

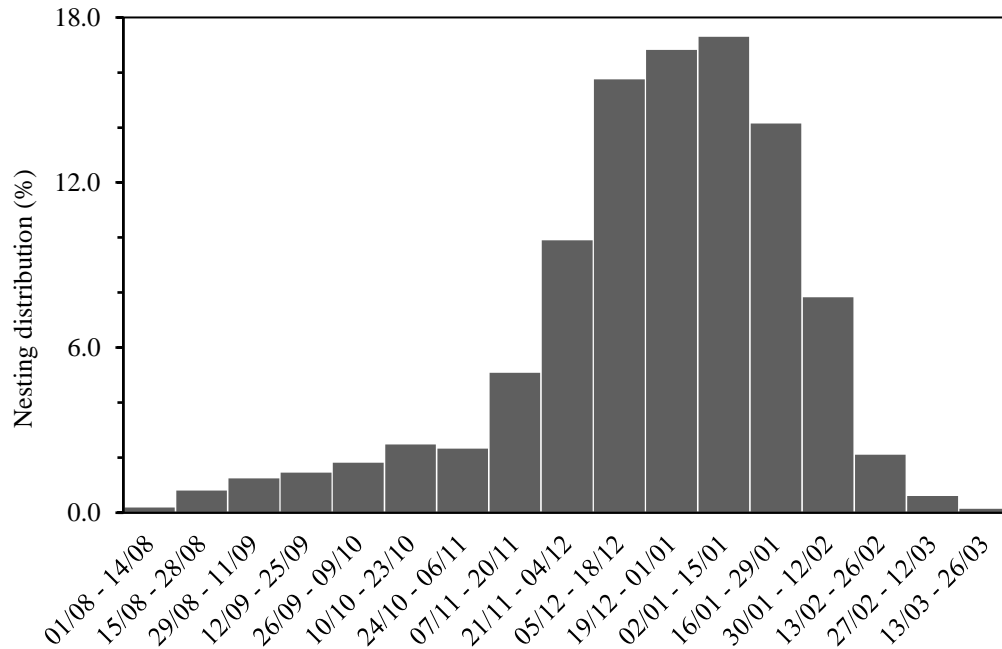


Figure 2: Mean temporal distribution of green sea turtles’ nests at Príncipe Island, by 14 day-intervals during eight consecutive nesting seasons (2015/16 to 2022/23).

3.2. Spatial distribution of green sea turtles’ nests

The spatial distribution of the nests varies markedly across the island and among the 36 beaches monitored (Figure 3). Praia Grande and Praia Infante denote the highest and the second highest percentages of nests per season, with 53.2% and 25.6%, respectively, representing together 78.8% (~ 80%) of the whole nest distribution (Figure 3). Praia Boi and Praia Seca represent $\pm 5\%$, followed by Praia Bumbo and Praia Cabinda that have $\pm 2\%$ each of the total nests in the island. Praia Cemitério, Praia Macaco, Praia Micotó and Praia Rio São Tomé represent only $\pm 1\%$ each. The remaining 26 monitored beaches (Table 2) (Praia Areia, Praia Banana, Praia Bombom, Praia Burra, Praia Caixão, Praia Cajú, Praia Campanha, Praia Esprainha, Praia Franguinha, Praia Lapa, Praia Margarida, Praia Maria Correia, Praia Marmita, Praia Montanha, Praia Novo, Praia Pedra Furada, Praia Pedrona, Praia Ponta Ramiro, Praia Popa, Praia Portinho, Praia Prainha, Praia Ribeira Izé, Praia Santa Rita, Praia Sundry, Praia Uva and Praia Yola) host $< 1\%$ of the annual green turtle nests, thus, 28% of the nesting beaches of Príncipe Island ($n = 36$), represent 97.2% of the total nests.

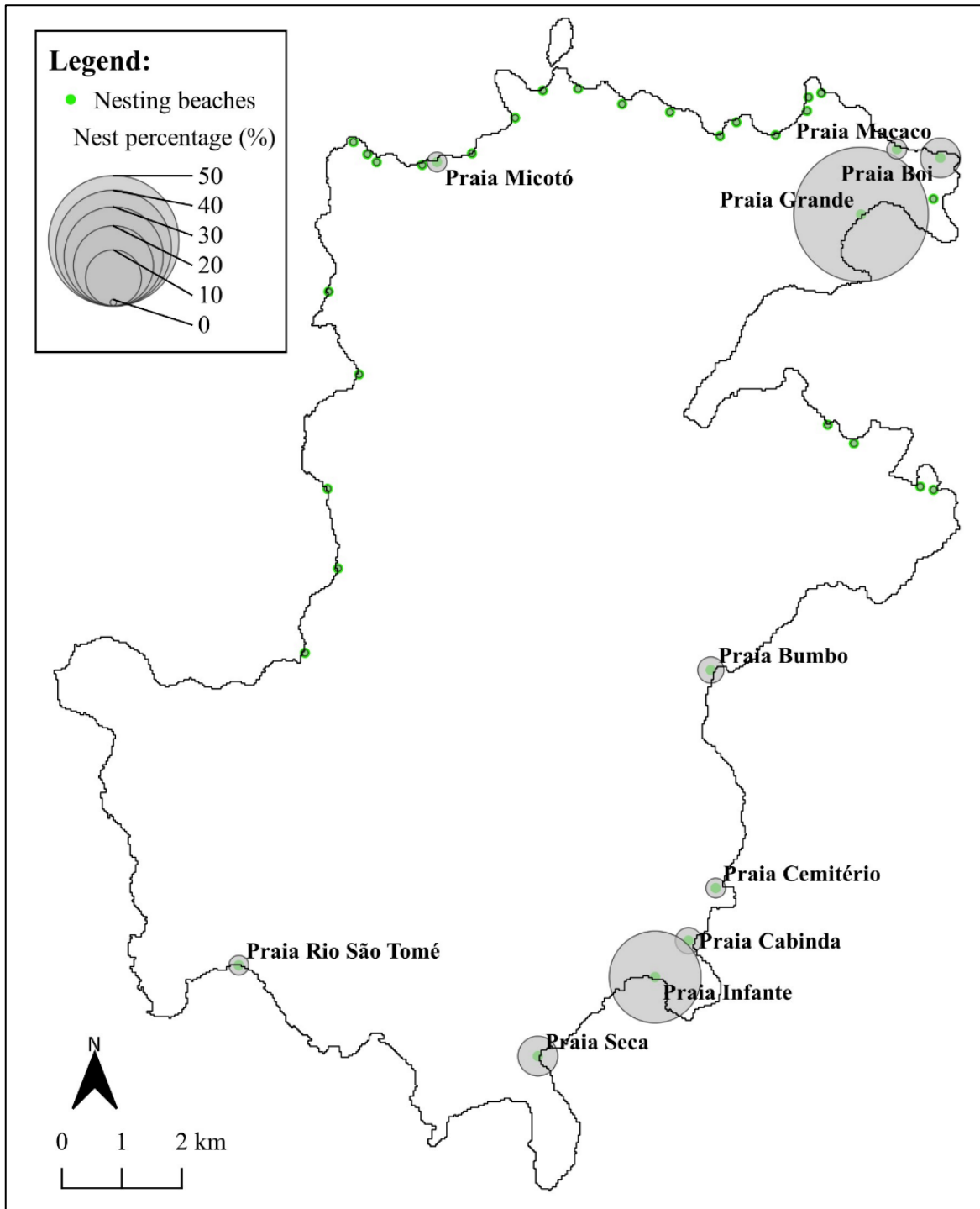


Figure 3: Location of the 36 beaches (portrayed by green dots) in Príncipe Island monitored for sea turtle nesting activities, and their respective mean percentage of green sea turtles' nests, across eight nesting seasons, from 2015/16 to 2022/23. Beaches not named in the picture represent a nesting percentage of around zero.

Table 2: Monitored beaches of Príncipe Island for sea turtle nesting activities and their respective length and number of nests (expected and observed).

Beach	Length (m)	Proportion of nesting length	Expected no. of nests	Mean no. of nests observed	χ^2	<i>df</i>	<i>P</i>
Praia Areia	260	0.02	26	1	4405.16	35	< 0.0001
Praia Banana	200	0.01	20	3			
Praia Boi	320	0.02	32	77			
Praia Bombom	680	0.05	68	3			
Praia Bumbo	800	0.05	80	34			
Praia Burra	760	0.05	76	0			
Praia Cabinda	400	0.03	40	25			
Praia Caixão	270	0.02	27	0			
Praia Cajú	180	0.01	18	1			
Praia Campanha	440	0.03	44	1			
Praia Cemitério	210	0.01	21	21			
Praia Esprainha	290	0.02	29	1			
Praia Franguinha	110	0.01	11	2			
Praia Grande	1400	0.09	139	788			
Praia Infante	1400	0.09	139	379			
Praia Lapa	620	0.04	62	0			
Praia Macaco	500	0.03	50	11			
Praia Margarida	90	0.01	9	2			
Praia Maria Correia	455	0.03	45	0			
Praia Ponta Marmita	50	0	5	0			
Praia Micotó	500	0.03	50	20			
Praia Montanha	450	0.03	45	3			
Praia Novo	90	0.01	9	0			
Praia Pedra Furada	210	0.01	21	1			
Praia Pedrona	180	0.01	18	1			
Praia Ponta Ramiro	70	0	7	0			
Praia Popa	150	0.01	15	0			
Praia Portinho	470	0.03	47	1			
Praia Prainha	50	0	5	6			
Praia Ribeira Izé	580	0.04	58	2			
Praia Rio São Tomé	535	0.04	53	8			
Praia Santa Rita	620	0.04	62	3			
Praia Seca	450	0.03	45	79			
Praia Sundy	520	0.03	52	4			
Praia Uva	50	0	5	4			
Praia Yola	520	0.03	52	1			
Total	14880	1	1481	1481			

Nesting spatial distribution seems to follow a tendency towards beaches located on the east coastline of Príncipe, where significant amounts of nests were found (Figure 3). From the Chi-square analysis ($\chi^2 = 4405.16$; $df = 35$; $p\text{-value} < 0.0001$) (Table 2) the calculated χ^2 showed to be greater than the critical value, implying that the distribution of nests was not random across all the available nesting habitat and that the numbers of nests per beach were not beach-length dependent (Table 2).

3.3. Nesting abundance trends for the island and for Praia Grande

A total of 11,847 green turtle nests were recorded during the eight consecutive seasons (from 2015/16 to 2022/2023) with an average (\pm SD) of 1481 ± 728 nests per year in all the nesting beaches of Príncipe Island. The number of nests showed a high annual fluctuation ranging from 411 (2018/19) to 2647 (in 2021/22), with a difference of 544.0% from the lowest season to the highest season. The number of nests through these years showed no increasing or decreasing trend since 2015/16 (*regression analysis*, $r^2 = 0.0687$, $p\text{-value} = 0.5307$) (Figure 4).

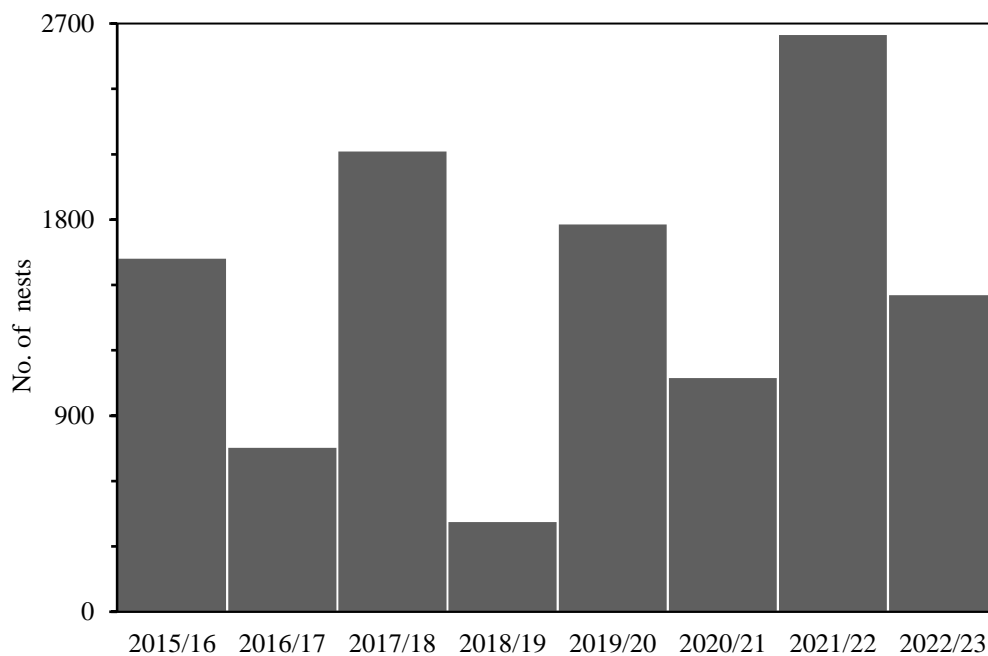


Figure 4: Number of green sea turtles' nests around Príncipe Island, from 2015/16 to 2022/23 nesting seasons.

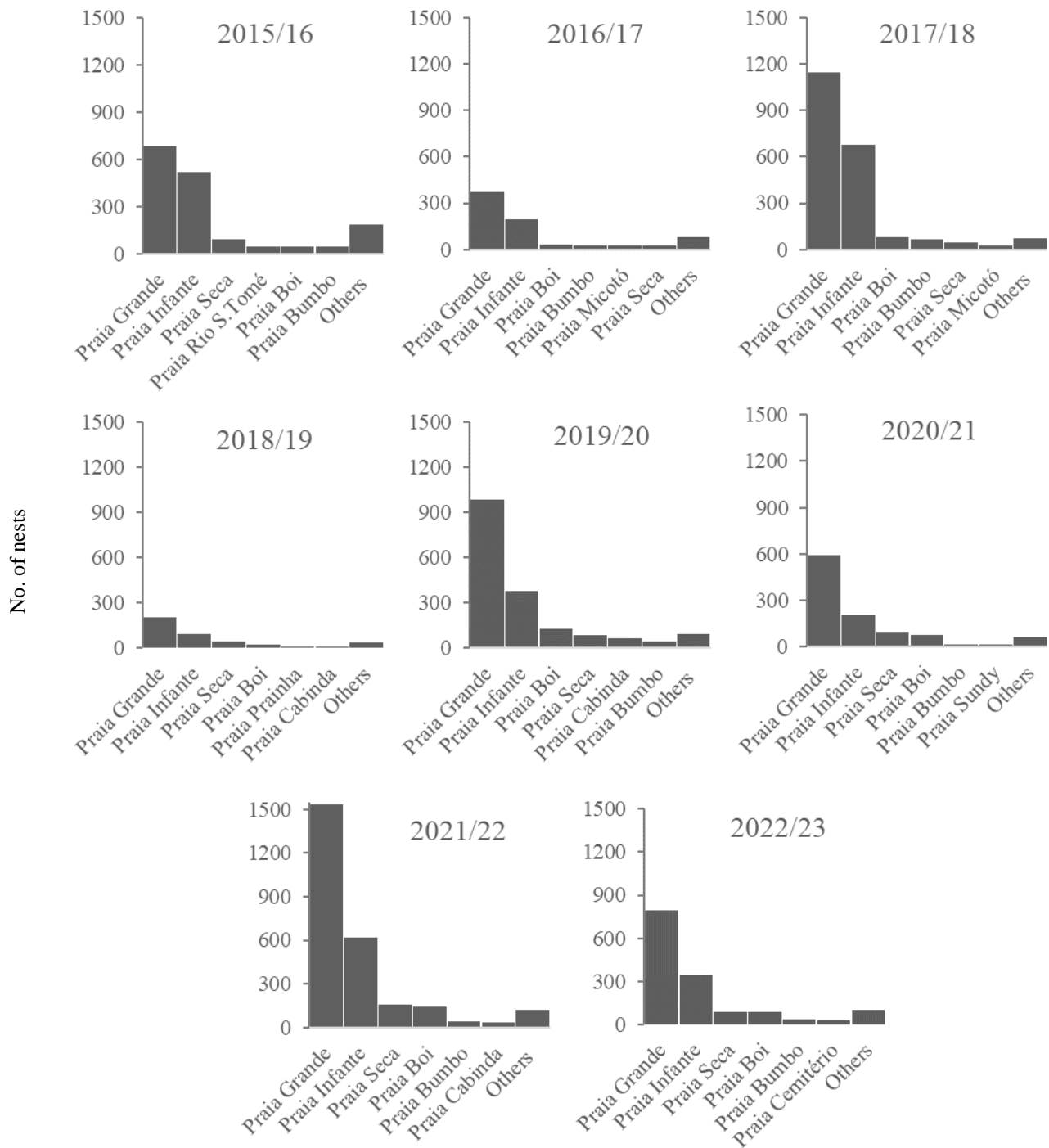


Figure 5: Spatial distribution of green sea turtles' nests during different nesting seasons (2015/16 – 2022/23) in Príncipe Island. The graphs represent the absolute number of nests in each beach, and each season exhibits the six beaches with the highest number of nests in that year.

In Príncipe, green sea turtles nest in most of the beaches, however, it is in Praia Grande where most females lay their clutches (Figure 3). Since 2015/16, this is the most used beach every nesting season (Figure 5). Praia Infante is also constant at second most visited. Praia Seca and Praia Boi tend to switch places through the seasons, keeping the third and fourth places (Figure 5).

For Praia Grande alone, our index beach, a total of 7899 green turtle nests were recorded during 16 consecutive nesting seasons (2007-2023). In this beach, the number of nests ranged from 41 (2007/08) to 1533 (in 2021/22), with a difference of 3639.0% from the lowest to the highest season (Figure 6). There was a significant increase in nest numbers between 2007/08 and 2022/23 (*regression analysis, $r^2 = 0.51$, p -value = 0.0018*) where 51% of the values fit the regression model (Figure 6).

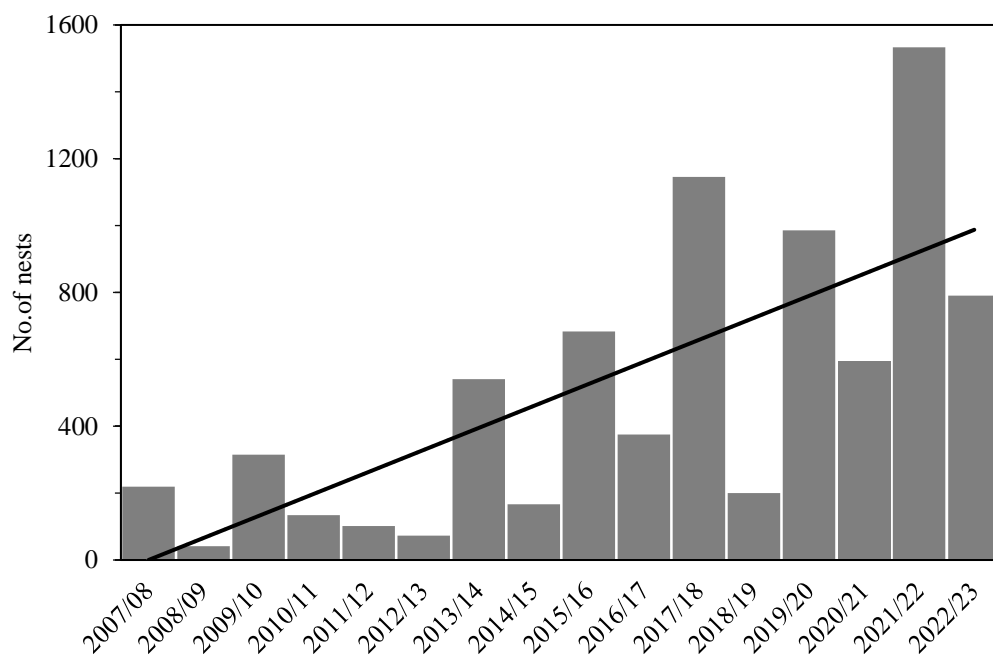


Figure 6: Number of green sea turtles' nests in Praia Grande, at Príncipe Island, during 16 consecutive nesting seasons: from 2007/08 to 2022/23. $r^2 = 0.51$, p -value = 0.0018.

The mean clutch frequency at Praia Grande, across all years, was 3.3 ± 1.8 (Ranging from 1 to 9 clutches/season) (Figure 7). Thus, we estimated the annual nesting female population abundance for the first and the last three years of monitoring by dividing the mean number of nests by the mean clutch frequency. From 2007/08 to 2009/10 the number of nests per year at Praia Grande was 192 ± 139 , equivalent to a population estimate of 58 ± 42 nesting green sea turtles per year (average \pm SD), and from 2020/21 to 2022/23 the average (\pm SD) was 972 ± 496 nests per season, equivalent to an estimated population size of 295 ± 150 nesting green sea turtles annually in Praia Grande.

Assuming a mean remigration interval of 3 years (Seminoff et al. 2015), the nesting population size of green turtles in Príncipe was estimated to be 174 ± 126 turtles between 2007/08 – 2009/10, and 884 ± 450 turtles, for the seasons between 2020/21 – 2022/23. These estimations result in an increasing of 407.3% from the first 3 nesting seasons surveyed, to the most recent.

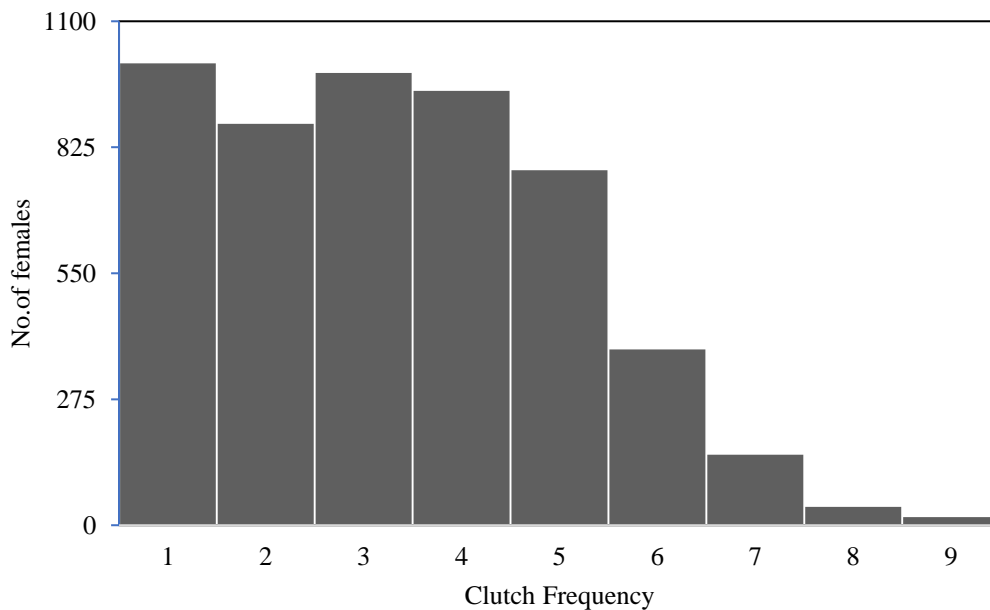


Figure 7: Observed clutch frequency of the nesting green sea turtles in Praia Grande, Príncipe Island.

3.4. Nesting female biometry and clutch size

A total of 4422 unique females were measured for their curved carapace length (CCL). These numbers refer to distinct individuals that have been measured throughout all nesting seasons, independently of the number of arrivals on land. Mean (\pm SD) CCL was 99.4 ± 5.8 cm (Range: 75 – 149 - imposed by our filtering of the data). The CCL distribution revealed that the majority of nesting green turtles in Príncipe, corresponding to 66.9% of the individuals ($n = 2957$), have between 95.0 and 105.0 cm. The CCL size class with the highest number of nesting females was between 100.0 and 105.0 cm, corresponding to 36.1% ($n = 1595$) (Figure 8).

Mean (\pm SD) clutch size was 111 ± 22 eggs/clutch (Range 40 – 180, imposed by our filtering of the data), with a substantial concentration between 100 and 130 eggs/clutch (61.4%, $n = 2650$). There was a statistically significant correlation between CCL and clutch size: *regression analysis*, $r^2 = 0.0039$, $p\text{-value} < 0.001$ (Figure 9), indicating that larger females tend to lay more eggs (Figure 9). This means that clutch size increases with curved carapace length despite the high amount of unexplainable variability. Bigger females have a higher impact in this trend, since between 90.0 and 110.0 cm of CCL exists a high variability of clutch sizes ranging between 40 and 180 eggs/clutch, whereas turtles with $CCL \geq 115$ cm always have approximately 100 eggs or above.

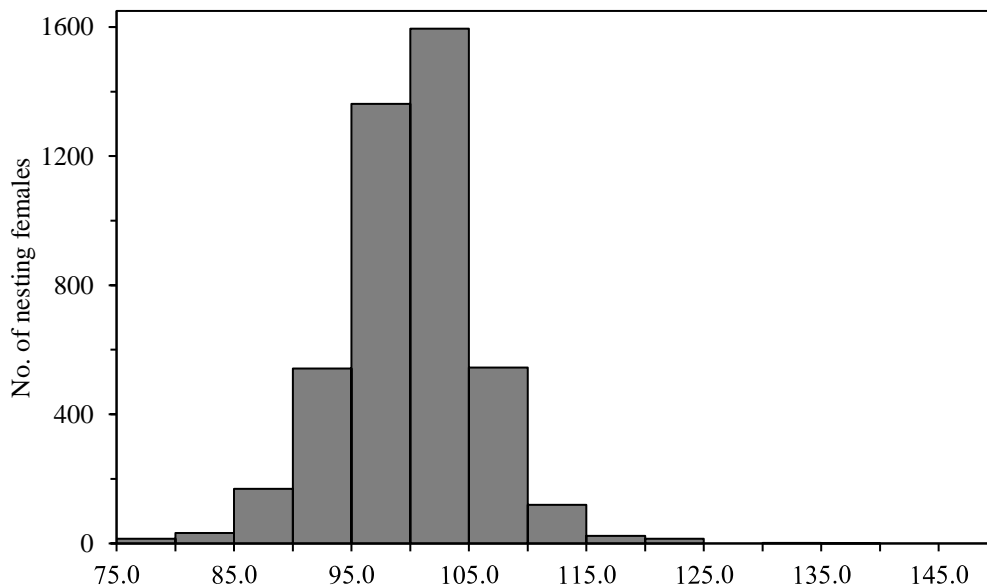


Figure 8: Curved carapace length (CCL) distribution of green sea turtle nesting females ($n = 4422$) from Príncipe Island, through the seasons of 2015/16 to 2022/23.

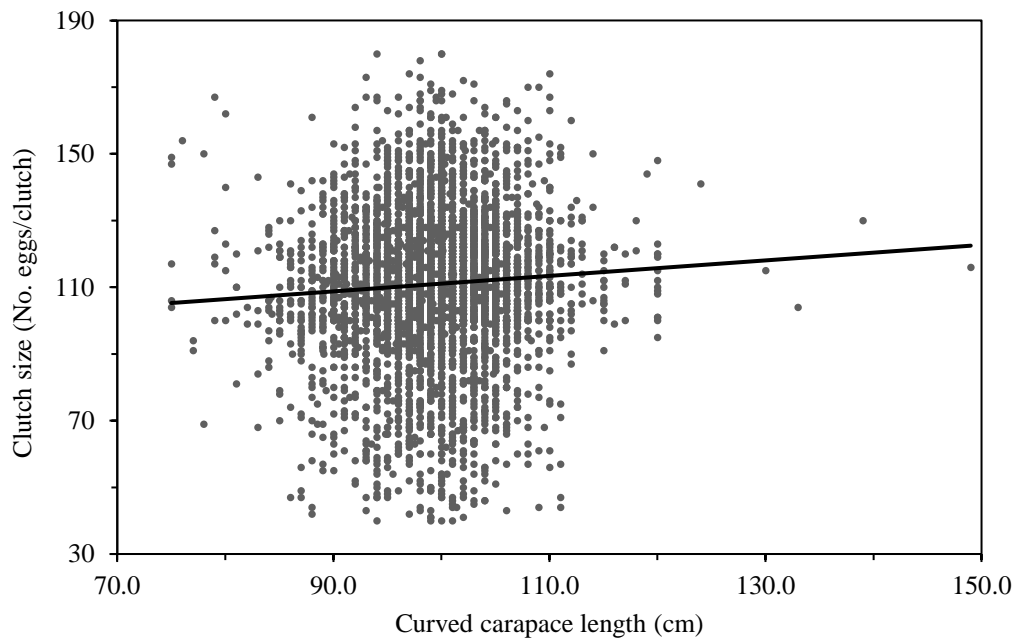


Figure 9: Correlation between curved carapace length (CCL) and clutch size (Number of eggs per clutch) in green turtles from Príncipe Island, Central Africa (n = 4422 nesting females). $r^2 = 0.0039$, p-value < 0.001.

3.5. Hatching Success

Hatching success (H%) ranged from $82.2 \pm 30.2\%$ (2015/16) to $97.7 \pm 22.4\%$ (2017/18), with an overall mean (\pm SD) hatching success of $88.9 \pm 5.2\%$ (Table 1) for all the island.

For Praia Grande, being the only beach where all nests are exhumed, it was possible to determine the success with and without the ‘lost nests’ (Table 3). Between 2015/16 and 2022/23, a mean (\pm SD) of $35.1 \pm 22.3\%$ of the marked clutches were lost every season, ranging between 21 and 722. The biggest percentage of ‘lost nests’ happened during the season of 2016/17 (84.5%) (Table 3). Under the assumption that all ‘lost nests’ have H% = 0, hatching success, for Praia Grande, ranged from $13.2 \pm 32.4\%$ (2016/17) to $80.6 \pm 34.1\%$ (2018/19) with a mean H% (\pm SD) of $58.4 \pm 21.9\%$ (Table 3). These ‘lost nests’, however, do not discard the possibility of the eggs having hatched, so this is an underestimation of the real value. Dismissing the ‘lost nests’ from the

hatching success estimation, H% in Praia Grande ranged from $89.8 \pm 20.9\%$ (2015/16) to $98.0 \pm 25.9\%$ (2017/18) with a mean H% (\pm SD) of $92.0 \pm 2.6\%$ (Table 3). To compare the differences between these approaches a Wilcoxon test for paired samples was used, since they did not follow a normal distribution. The statistical analysis ($V = 36$, p -value < 0.01) indicated that the means of the two approaches are significantly different showcasing a variation of almost 34% between them (33.6%). This highlights the importance of accounting for lost nests when denoting the hatching success of a beach/location.

Table 3: Hatching success (H%) (\pm SD) of green turtle clutches at all nesting beaches of Príncipe Island (including Praia Grande), and only at Praia Grande. In Praia Grande, hatching success was estimated both excluding ‘lost nests’ and including these with H%=0. These estimates represent only the hatching success associated with abiotic factors, ignoring clutch predation.

	All Nesting Beaches			Praia Grande							
	H%	SD	n	Without ‘lost nests’			With ‘lost nests’			‘Lost nests’	
				H%	SD	n	H%	SD	n	%	n
2015/16	82.2	30.2	737	89.8	20.9	401	55.4	46.7	650	36.5	249
2016/17	82.4	27.3	93	91.9	7.3	53	13.2	32.4	370	84.5	317
2017/18	97.7	22.4	1210	98.0	25.9	783	66.9	50.4	1146	31.5	361
2018/19	85.8	25.5	241	91.6	17.5	154	80.6	34.1	175	10.5	21
2019/20	90.3	17.5	1232	90.3	20.4	759	75.3	38.4	910	15.3	151
2020/21	90.8	17.4	802	91.1	14.9	435	74.8	37.5	530	16.0	95
2021/22	90.5	20.4	1475	90.3	20.4	742	45.8	47.2	1464	47.1	722
2022/23	91.6	18.6	802	93.0	15.3	458	55.2	47.2	772	39.7	314
Average	88.9	5.2		92.0	2.6		58.4	21.9		35.1 \pm 22.3	278.8 \pm 201.0

Hatching success varied significantly among nesting seasons (one-away ANOVA, $F = 41.58$, 13.05 and 113.11, respectively, p -value < 0.01) (Table 3). For all nesting beaches ($r^2 = 0.255$, $F = 2.053$, p -value = 0.202) and Praia Grande without and accounting for ‘lost nests’ ($r^2 =$

0.007 and 0.058, $F = 0.043$ and 0.368 , $p\text{-value} = 0.843$ and 0.567 , respectively) the mean H% showed no significant increasing or decreasing trend across the eight consecutive years for all the three estimates (all beaches, and Praia Grande using both approaches).

3.6. Clutch predation

During nest exhumation, the number of eggs found inside predated clutches ranged between 0 to 172, being found partial and total predation (= 0) evidence. Various sea turtle clutch predators were identified throughout the years, in Príncipe Island (Table 4), namely the African civets (*Civettictis civetta*), São Tomé Land Crabs (*Johnngarthia weileri*) and Tufted Ghost Crabs (*Ocypode cursor*), dogs, ants and pigs.

Table 4: Clutch predation of green sea turtle’s nests between 2015/16 to 2022/23, from all nesting beaches of Príncipe Island, in absolute values (n) with the respective average (\pm SD) and correspondent percentage. Proportion of predated nests = total predated nests/total exhumed nests.

	2015/ 16	2016/ 17	2017/ 18	2018/ 19	2019/ 20	2020/ 21	2021/ 22	2022/ 23	Mean \pm SD	%
Predators										
African civet	1	1	-	-	1	-	-	1	1.0 \pm 0.0	1.2
Ants	31	10	2	-	-	-	-	-	14.3 \pm 15.0	16.5
Dog	31	2	-	13	129	59	111	22	52.4 \pm 49.7	60.2
Human	3	-	-	-	1	1	5	2	2.4 \pm 1.7	2.8
Pig	-	-	-	-	-	1	51	7	19.7 \pm 27.3	22.6
São Tomé Land Crab	25	2	-	22	6	20	2	2	11.3 \pm 10.5	13.0
Tufted Ghost Crab	-	-	-	-	8	38	26	17	22.3 \pm 12.8	25.5
Unspecified	7	11	-	3	6	6	11	-	7.3 \pm 3.1	8.4
Total predated nests (n)	98	26	2	38	151	125	206	51	87.1 \pm 70.2	5.4
Total exhumed nests (n)	836	120	1212	279	1383	927	1681	853	911.4 \pm 526.5	61.5
Predated clutches (%)	11.7	21.7	0.0	13.6	10.9	13.5	12.3	6.0	11.2 \pm 6.2	

Predation was substantially variable across the seasons, ranging from 206 clutches in 2021/2 to 2 clutches in 2016/17. On average (\pm SD), 87.1 ± 70.2 nests were predated each season, corresponding to $11.2 \pm 6.2\%$ of the total clutches laid (Table 4).

The most impactful predators that appear to be consistent and present since 2015/16 are the stray dogs that can be found all around the island (Table 4). They alone represent 60.2% of all predation causes, followed by tufted ghost crabs responsible for 25.5% of clutch predation events. Pigs have been an increasing concern at Praia Boi, where in 2020/21 they become the main predator (22.6%) (Table 4). In the nesting season of 2022/23, however, preventive measures were developed to protect the clutches from being depredated by pigs at Praia Boi. This resulted in a decrease of predated nests.

Exhumation was only conducted in 61.5% of the corresponding to an average (\pm SD) of 911.4 ± 526.5 nests each nesting season (Table 4).

At Praia Grande the predation results are analogous with those observed for the totality of the beaches of Principe Island (Table 5). The impacts of the stray dogs are more visible being the cause for 73.4% of clutch predation and with an average (\pm SD) of 26.7 ± 21.8 nests predated each nesting season. Tufted ghost crabs were also responsible for a high percentage of predation, equal to 37.4%. Pigs are not a concerning problem in Praia Grande. There are 10.0% of predated nests for which the predators are not specified. Thus, other types of predators might be present. Praia Grande showed a mean (\pm SD) predation percentage of $8.0 \pm 4.4\%$, with an average (\pm SD) of 36.1 ± 28.2 nests predated per season (4.4%) and a total of 509.6 ± 273.1 exhumed nests per season (64.6%) (Table 5). The mean (\pm SD) predation percentages for the whole island as well as for Praia Grande, did not show statistically significant differences between nesting seasons (one-away ANOVA, $F = 0.24$, $p\text{-value} = 0.96$).

Table 5: Clutch predation of green sea turtle’s nests from 2015/16 to 2022/23 at Praia Grande (index beach) of Príncipe Island in absolute values (n) with the respective average (\pm SD) and correspondent percentage. Proportion of predated nests = total predated nests/total exhumed nests.

	2015/ 16	2016/ 17	2017/ 18	2018/ 19	2019/ 20	2020/ 21	2021/ 22	2022/ 23	Mean \pm SD	%
Predators										
Dog	20	2	-	11	64	30	46	14	26.7 \pm 21.8	73.9
São Tomé Land Crab	8	-	-	13	4	5	-	-	7.5 \pm 4.1	20.8
Tufted Ghost Crab	-	-	-	-	6	26	17	5	13.5 \pm 10.0	37.4
Unspecified	5	3	-	-	2	2	6	-	3.6 \pm 1.8	10.0
Total predated nests (n)	33	5	0	24	76	63	69	19	36.1 \pm 28.2	4.4
Total exhumed nests (n)	434	58	785	179	835	498	811	477	509.6 \pm 273.1	64.6
Predated clutches (%)	7.6	8.6	0.0	13.4	9.1	12.7	8.5	4.0	8.0 \pm 4.4	

4. Discussion

This study offers the first comprehensive overview of the nesting biology of the green sea turtle population of Príncipe Island. It delivers key insights into the complex dynamics of this genetically significant rookery (Hancock, 2019), which belongs to one of the lesser-known populations in the Gulf of Guinea. Drawing from early monitoring data, this study examines the spatiotemporal distribution of green turtle nests in Príncipe Island, the reproductive output and the impact of clutch predation. Praia Grande, the island's primary nesting site, has consistently shown the highest activity and has seen a rise in nests over the years. These findings provide crucial information on the conservation challenges and opportunities for green sea turtles on Príncipe.

4.4. Temporal and spatial distribution:

The temporal distribution of green sea turtle nests on Príncipe Island peaks between early December and the end of January, overlapping with one of the island's dry seasons, *Gravaninha*, which lasts from mid-December to March. Despite this peak, the overall nesting season extends from September to April, similar to São Tomé Island (Ferreira-Airaud et al., 2024). In most sea turtle populations, nesting occurs during the warmest months (Miller, 1996), which is consistent with the findings for the Príncipe population. This pattern differs from that of Poilão (Cтры et al., 2002a), where peak nesting occurs from August to September during the rainy season, and Ascension Island, where (Mortimer & Carr, 1987) found that the peak season (March) coincided with the highest rainfall and temperatures. The latter study suggested that wetter conditions might make digging nests easier, as dry sand is more challenging to dig a nest. However, no solid evidence supports this hypothesis, and (Godley et al., 2001) proposed a link between nesting magnitude and air temperature, showing that in non-nesting months, sand temperatures were near the lower thermal tolerance limit for turtle embryos. This suggests that turtles may have adapted to nest during periods of highest sand temperatures, avoiding cooler months when nest temperatures could be too low. The rainy season can alter beach conditions, such as sand temperature and moisture, which are crucial for nest construction and may also influence demographic factors like sex ratios (Casale et al., 2000; Chan & Liew, 1995; Mrosovsky et al., 1984; Rebelo et al., 2012). Looking forward, climate change could impact these distribution patterns due to its effect on environmental conditions (Fuentes et al., 2010, 2011; Glen & Mrosovsky, 2004). Changes in rainfall patterns could alter beach characteristics and affect the spatial distribution of nesting sites (Chaloupka, Work, et al., 2008; R. Patrício et al., 2014). Turtles may begin to prefer locations that provide better conditions for nest success, which could become increasingly important as climate change influences the timing and amount of rainfall.

On São Tomé Island, green turtles similarly experience peak nesting activity in November, December, and January (Graff, 1996). Hancock (2019) found no genetic differences between the green turtles of São Tomé and Príncipe Islands, indicating that females from both islands belong to the same population or rookery. This understanding of nesting dynamics on Príncipe supports the view that the turtles of the archipelago represent a single population.

Nesting on Príncipe Island is unevenly distributed, with some beaches offering more favourable conditions for green sea turtle nesting, likely due to factors such as sand quality, beach slopes, or reduced predation risks (R. L. Ferreira et al., 2018, 2019; A. R. Patrício et al., 2018). Praia Grande in the north and Praia Infante in the south account for the highest nesting activity, representing 78.8% of nests on the island. Since 2015/16, these beaches have consistently hosted the majority of nesting, and according to Loureiro et al. (2011) and Ferreira et al. (2019), they hosted 55% of green turtle clutches between 2009 and 2010 (Ferreira et al. 2019), showing that these preferable beaches go back in time.

Praia Grande is characterized by white sand and a bay that protects the coastal area, while Praia Infante has black fine sand, a rocky shore, strong currents, and a high risk of inundation (Ferreira et al. 2019). Female green turtles in Príncipe tend to favour the island's eastern side for nesting, likely due to geographic factors that affect beach exposure. A similar trend is observed on São Tomé Island, where green turtles nest along the northern, eastern, and southern coasts, avoiding the western coastline due to its rocky beaches. Western beaches are more exposed to the Atlantic Ocean, which results in fewer sandy areas and steeper slopes, providing fewer suitable nesting sites (Godley et al., 2001). Protected beaches like Praia Grande experience higher nesting activity, however, this does not always mean that these beaches have the best conditions. Often, the remoteness of the beaches reduces human disturbance, including poaching and turtle killings, contributing to their use by nesting turtles. For example, Praia Infante is difficult to access by land, which limits human interference, despite its challenging nesting conditions due to high wave exposure and rocky shores.

In Ascension Island, the suitability of nesting beaches is partly influenced by offshore seabed topography, with beaches having fewer offshore rocks hosting more nests (Mortimer, 1990; Mortimer & Carr, 1987). Sand texture also plays a role, as turtles can dig nests more easily on beaches with smaller sand particles (Godley et al., 2001; Mortimer, 1990). The current nesting distribution on Príncipe remains consistent with patterns observed from 2007 to 2010, with the same major beaches holding most of the nests (Loureiro et al., 2011). Nesting abundance is not related to beach length, suggesting that some beaches provide better conditions for turtle nesting. Furthermore, the consistently higher nesting numbers at Praia Grande each season suggest that this beach provides a more favourable environment for nesting turtles and their clutches.

Female turtles often return to the same beaches during their reproductive cycle, showing loyalty to those shorelines. This reinforces the idea that Praia Grande and Praia Infante offer the best conditions for egg development, likely including favourable biotic and abiotic factors. However, it is still unclear whether the same females return to Praia Grande each year or if they alternate between nearby beaches. While it is likely that many turtles remain faithful to Praia Grande, some degree of movement between beaches may exist.

As noted by Plotkin (2003), site fidelity is common among green sea turtles. Praia Grande has shown strong site fidelity, with some females laying up to nine clutches there in a single nesting season. Nevertheless, instances of females nesting on other beaches have been recorded. For example, a turtle tagged at Praia Grande in 2008 was observed nesting 15 km away in 2010, and another turtle tagged 13.5 km away from Praia Grande in 2006/07 was later found nesting at Praia Grande in 2009/10 (Loureiro et al., 2011). These observations suggest that, while there is high site fidelity, some turtles nest at nearby beaches as well, highlighting the need for more comprehensive monitoring and tagging.

4.2. Nesting Abundance and trends

Fundação Príncipe has played a crucial role in monitoring green sea turtles on Príncipe Island. Since its implementation in 2015, it has collected valuable and more accurate data on nesting activities, leading to improved and more reliable results. Before 2015, inconsistencies in conservation teams and organizations made the data less reliable. Therefore, the observed increase in nesting abundance could be due to standardized monitoring and constant daily surveys, or an actual population growth. Thanks to the work of Fundação Príncipe, long-term monitoring on the island may have positive impacts on the conservation of green sea turtles.

Over eight consecutive seasons, Príncipe Island has shown no significant increase in green turtle nesting activity. While green turtle nesting on the island has been documented for years, this study only includes data from 2015 onward for the whole island, which is a relatively short period in the lifecycle of sea turtles to determine long-term trends in nest numbers. The 2015/16 nesting season was particularly strong, but without earlier data, it is impossible to show any growth trends from previous years. Recent studies by Ferreira-Airaud et al. (2022) indicated that Príncipe likely hosts a significant portion (65%) of the São Tomé and Príncipe archipelago's green turtle

population. On São Tomé Island, between 2014 and 2022, 6,092 clutches were recorded with an average of 762 ± 404 nests per year (Ferreira-Airaund et al., 2024). In Príncipe, during the same period (2015–2023), 11,847 nests were recorded, with an average of $1,481 \pm 728$ nests per year. This discovery is critical for creating effective conservation strategies, including the protection of nearshore inter-nesting areas, namely through Marine Protected Areas (MPAs).

When analysing a longer time series for Praia Grande, the island's most significant nesting site and our index beach (2007–2023), a total of 7,899 nests were recorded and there was a significant increase in nest numbers over the 16 seasons. This rise may be due to successful conservation efforts or favourable conditions attracting more nesting females. The protection of foraging areas along Africa's west coast and a reduction in predator pressure due to declining shark numbers may also contribute to this trend (Heithaus et al., 2014). Clutch frequency, a critical parameter for reproductive output, has ranged from one to nine clutches per year at Praia Grande from 2015/16 to 2022/23, with an average of 3.3 clutches. This is comparable to other green turtle populations, where Miller (1997) found an average of 2.93, and Broderick et al. (2003) reported 3.0 for Cyprus. However, Príncipe's clutch frequency is higher than that of São Tomé Island (2.5 ± 0.9), where clutches ranged from one to six per female (Ferreira-Airaund et al., 2024). Loureiro et al. (2011) estimated clutch frequency for Praia Grande between 2007/08 and 2009/10, observing a maximum of seven clutches and an average of three. While clutch frequency remained stable, it seems that females are laying more clutches per season in recent years. Clutch frequency helps estimate the nesting female population, which has increased from approximately 58 females per year in the early years of monitoring to around 295 in recent seasons. This increase may also be influenced by greater survey efforts, resulting in more reports of nesting events.

Remigration intervals, typically ranging from 2 to 5 years (Hirth, 1980; Seminoff et al., 2015), suggest that a female green turtle may nest in 3 to 11 seasons over her lifetime, with an estimated 3 nests per season and 100 eggs per nest (Hirth, 1980; Seminoff et al., 2015). Although these are rough estimates, they provide a basis for understanding reproductive efforts. Troëng & Chaloupka (2007) found that remigration intervals at the Tortuguero rookery in Costa Rica are usually 2 or 3 years, though these intervals may be shorter due to environmental factors. In Cyprus, Broderick et al. (2001) observed that females at Alagadi Beach often shift between remigration intervals. Remigration intervals for Príncipe have not yet been determined, but Ferreira-Airaud et

al. (2024) used a 2.3-year interval for São Tomé, estimating a population of 736 nesting females. For Príncipe, this study used a 3-year interval (Seminoff et al., 2015), estimating a population of 884 nesting green turtles for the last three nesting seasons.

In 2006, Formia et al. (2006) estimated 75 to 100 nesting green turtles on Praia Grande based on unpublished data from the 1998/99 and 1999/00 nesting seasons. Loureiro et al. (2011) estimated 88 and 122 adult female nesters during the 2007/08 and 2009/10 seasons, respectively. If these estimates were accurate, it reinforces that the nesting population has increased. Between 2020/21 and 2022/23, six to seven times more turtles nested than between 2007/08 and 2009/10, reflecting the overall increase. However, because green turtle nesting numbers can vary from year to year (Balazs, 1976; Hays & Scott, 2013; Mortimer & Carr, 1987) long-term monitoring is still necessary to assess changes in the Príncipe population. The São Tomé and Príncipe population belongs to the South Atlantic (SATL) genetic group, which includes populations from Atol das Rocas/Fernando de Noronha (Brazil), Trindade (Brazil), Bioko (Equatorial Guinea), Ascension Island, and Poilão (Guinea-Bissau). However, the São Tomé and Príncipe rookery is genetically distinct from the others in the Atlantic, including the nearby Bioko Island (Seminoff et al., 2015). An estimate for Ascension Island's green turtle population suggests that these turtles reach reproductive maturity at 17 years (Godley et al., 2001), highlighting the importance of collecting nesting data over a longer period to observe true population trends and the effectiveness of conservation efforts. Longer monitoring periods will allow scientists to track turtles hatched on Príncipe's beaches, providing insights into their nesting fidelity and conservation status.

4.3. Nesting female biometry and clutch size

Reproductive data for nesting green turtles has never been documented for Príncipe Island before. The analysis of curved carapace length (CCL) showed that the adult population is relatively homogenous in size, with a mean of 99.4 ± 5.8 cm. This is consistent with findings from São Tomé Island, where the average CCL is 99.1 cm, with a range between 72.3 to 127.0 cm, also in line with this study (Ferreira-Airaud et al., 2024). This population has the nesting females among the smallest reported in the Atlantic, where small sizes at maturity could be attributed to years of harvesting (Balazs, 1976; Balazs & Chaloupka, 2004; Chaloupka & Limpus, 2001; Van Houtan & Kittinger, 2014). However, other factors such as ecosystem characteristics, food availability, and

migration patterns may also affect average turtle size (Hays & Scott, 2013; Seminoff et al., 2015). Climate change-driven ecological changes in foraging areas might also play a role. Research has shown that reductions in body size among sea turtle populations are linked to changes in ocean productivity and foraging habitat quality, impacting reproductive output and overall fitness (Broderick et al., 2003b; Johnson' And & Ehrhart, 1996; Le Gouvello et al., 2020). Therefore, a thorough assessment of foraging areas in Príncipe is necessary. Other green turtle populations in the South Atlantic, such as those in Trindade Island, Brazil, with a CCL of 115.2 cm, and Atol das Rocas, Brazil, with 115.9 cm, show significantly larger carapace lengths than those in Príncipe.

In this study, most results fell within a specific range for CCL and clutch size. Extreme values were excluded to eliminate obvious errors in measurements or recordings, leaving a CCL range of 75-149 cm and a clutch size range of 40-180 eggs. Most likely, erroneous values on clutch sizes could have resulted from patrollers counting two nests as one during periods of high nesting activity, undocumented predation, or disturbances caused by the monitoring team, which may lead to clutch abandonment. Larger females were generally associated with larger clutch sizes, but this relationship showed considerable variability, particularly among females in the 90-110 cm CCL range, potentially leading to underestimation of values.

The average clutch size in Príncipe is 111 ± 22 eggs per clutch, which is lower than Poilão's average of 131.2 eggs (Catry et al., 2009b) and similar to São Tomé Island's average of 117.3 eggs (Ferreira-Airaud et al., 2024). Hirth (1980) found that the number of hatchlings produced by a female per clutch ranges from 67 to 138 and that there is a significant correlation between clutch size and carapace length, with larger females typically laying larger clutches. This aligns with the findings in this study, where a significant correlation between CCL and clutch size was observed. The smaller CCL in the São Tomé and Príncipe green turtle population suggests that their clutch sizes are also expected to be smaller.

4.4. Hatching success

The overall hatching success rate on Príncipe Island ($88.9 \pm 5.2\%$) is comparable to values reported for other green turtle rookeries, such as Ascension Island (57.0-85.0%) as described by Broderick et al. (2001) and Quintana Roo, Mexico (91.6%) as noted by (Santos et al., 2017) However, it exceeds the hatching success of other populations, such as Poilão in Guinea-Bissau

(67.9%; (Cтры et al., 2002b), Akyatan Beach in Turkey (58.0-67.0%; Yılmaz et al., 2022) and Tortuguero in Costa Rica (42.0–57.0%; (Fowler, 1979).

At Praia Grande, the hatching success varied depending on whether 'lost nests' were included in the analysis. Assuming a 100% mortality rate for all lost nests likely underestimated the true hatching success, as lost nests likely include a combination of disturbed and undisturbed clutches. Excluding these lost nests, the hatching success remained consistently above 90%. However, when lost nests were included, the average hatching success dropped to $58.4 \pm 21.9\%$. Despite this, Praia Grande still had seasons where hatching success exceeded 60% in 4 out of 8 nesting seasons, underscoring the significance of this beach. It also highlights the importance of accurately accounting for lost nests to provide more precise hatching success estimates. Even with a higher percentage of lost nests, Praia Grande still falls within the ranges observed at other sea turtle rookeries, showing that it remains a favourable nesting site. It is also essential to consider that predation significantly impacts hatching success, and predated clutches were excluded from these calculations. The lack of data on predated nests can lead to an underestimation of clutch size. Stokes et al. (2024) found that frequent predation by crabs can lead to lower reported clutch sizes. However, nest predation rates on both Príncipe and Praia Grande have been low, adding confidence to the reliability of the data. Additionally, an increase in the number of nests on Príncipe, particularly at Praia Grande, has not resulted in a decline in average hatching success rates. This suggests that, in most years, the turtles have not yet exceeded the available nesting space, preventing overcrowding.

4.5. Clutch predation

Predation has been identified as a significant threat to nesting success across all nesting beaches on Príncipe Island, with an average of 11.2% of nests predated each season. The variation in predation rates between seasons and beaches suggests that effective predator management is crucial to improving nesting success. For instance, pigs have emerged as a key predator on Praia Boi, where targeted control measures have successfully reduced nest predation in recent years.

Stray dogs have consistently been the primary predators, which is likely related to the proximity of some nesting beaches to human communities, despite these beaches being uninhabited. The island has implemented sterilization campaigns to address this issue, typically

conducted twice a year. These campaigns have reduced dog populations, resulting in alternating high (2019/20 and 2021/22) and low (2018/19, 2020/21, and 2022/23) predation rates in recent years. However, inconsistent monitoring, particularly during the 2016/17 and 2017/18 nesting seasons, may have led to incomplete data, as it is unlikely that predation was absent in any year. More recent nesting seasons have seen improvements in monitoring consistency. Some predated clutches might also be linked to lost nest locations, contributing to uncertainties in data accuracy. Predation rates fluctuated from season to season, and although the average rate is considered low ($11.2 \pm 6.2\%$), it may reflect insufficient monitoring coverage of all nesting areas on Príncipe. Poaching remains a concern, particularly on less-monitored beaches, even as an illegal practice on the island it still occurs, especially near poorer communities.

The absence of predation data in certain years raises questions about the causes. Seasons without predation data are rare and likely indicate monitoring challenges. For example, if there was no dog predation in 2017/18 and 2018/19, could this also mean a lack of crab predation. In the Bijagós, when monitor lizards predate on nests, crabs often exploit the excavations to feed on the eggs (Ferreira, 2012). This pattern might apply in Príncipe, where if dogs do not excavate nests, crabs may also reduce predation. In contrast, in Cabo Verde, ghost crabs are the primary predators of sea turtle eggs and do not rely on other predators' excavations (Martins et al., 2022).

In sea turtles, the risk of nest predation is primarily linked to the detectability of the nests (Leighton et al., 2009). Predators may detect nests through disturbances in the sand caused by nesting turtles and olfactory cues released by the buried eggs (Leighton et al., 2009). These olfactory cues can persist after surface cues have disappeared, which may explain why clutches are often predated within 10 days of oviposition (Leighton et al., 2011). Habitat structure also plays a significant role in the predation risk of sea turtle nests (Fowler, 1979; Leighton et al., 2011). Beach vegetation is a key factor, particularly for predators that rely on vegetation as both a refuge and a hunting ground (Ferreira, 2012; R. L. Ferreira et al., 2019; Fowler, 1979). More data on clutch locations would help assess this relationship. Studies have shown that the number of predated eggs varies between habitats and different areas of the beach. For instance, eggshells are more easily found in low-height herbaceous areas compared to shrubs or dense forests, leading to higher predation rates in herbaceous areas. This characteristic might influence beach preference for nesting, although it still requires assessment for Praia Grande.

3.6. Suggestions for the future

This study emphasized some lacks in the monitoring and data collection, which may lead to misinterpretations of the real population status and characteristics. It is necessary to address the problems in order to improve conservation efforts and find solutions for these issues. Some suggestions for future surveys rely on: - Counting the number of eggs during oviposition, so clutch size numbers are known and do not induce in errors for hatching success and clutch predation. Do this in a sample of around 100 or more nests, and thoroughly monitor these nests during the season to assess further information. Another option is to choose randomly fresh clutches and carefully open the nest and count how many eggs are inside, closing it right after; - Increase the efforts during exhumation processes in all the recorded nests, throughout the island and all beaches. This will allow to have a bigger range of data and better information on how female turtles nest and use the other Príncipe beaches, as well as the surrounding areas.

5. Conclusions

This study provided important insights about the nesting biology of green turtles' population of Príncipe Island. Through long-term monitoring, it was possible to observe the spatial and temporal nesting patterns of these turtles, as well as the nesting female reproductive aspects, and conservation challenges faced by these animals.

The green sea turtle population of Príncipe followed a temporal distribution pattern that aligned with one of the dry periods (*Gravaninha*) of the island and coincided with the São Tomé population. Peaking between December and January, green turtles showed a preference for the eastern side of the island and a strong site fidelity, probably returning to the same nesting sites every year. However, movements between nearby beaches were observed, emphasizing the need for comprehensive tagging and monitoring. Praia Grande and Praia Infante have shown this fidelity, being the favourite nesting beaches and possessing almost 80% of all nesting activity observed. With time, climate change can also impact nesting patterns due to shifts in rainfall and beach characteristics, that can influence the future distribution of nesting sites, with turtles possibly favouring beaches with better environmental conditions.

For eight consecutive years, no significant increase in the green turtle nesting population was observed, due its small time period, however, Praia Grande, considered as the index beach, revealed consistent growth in nesting activity over 16 consecutive nesting seasons. It remains uncertain if this is a reflection on actual population growth or if it was influenced by the higher survey efforts since the improved and standardized monitoring by Fundação Príncipe since 2015.

For Príncipe, an estimated 884 nesting green turtle population was obtained for the last three seasons, which revealed to be six to seven times more turtles than from the nesting seasons of 2007/08 – 2009/10. Long-term data analysis is still in need for determining definitive trends.

Nesting population of Príncipe showcased mean curved carapace lengths smaller compared to other Atlantic population, but similar to São Tomé nesting females. Reportedly among the smallest reported nesting females in the Atlantic Ocean, clutch size also proved to be slightly lower from near green turtle populations and similar to São Tomé island's average, likely due to the smaller size of nesting females.

Hatching success was relatively high, when compared to other nesting populations, which may indicate favourable nesting conditions. Underestimations might have been made, since important data was missing like the percentage of 'lost nests' of the island, and detailed information of predation numbers. Predation was primarily made by dogs and crabs, remaining a significant threat to nesting success.

This study highlights the importance of continued conservation efforts, detailed monitoring, and addressing environmental challenges to ensure the long-term survival of green sea turtles ON Príncipe Island, eluding for monitoring problems that can influence this analysis.

6. Appendix

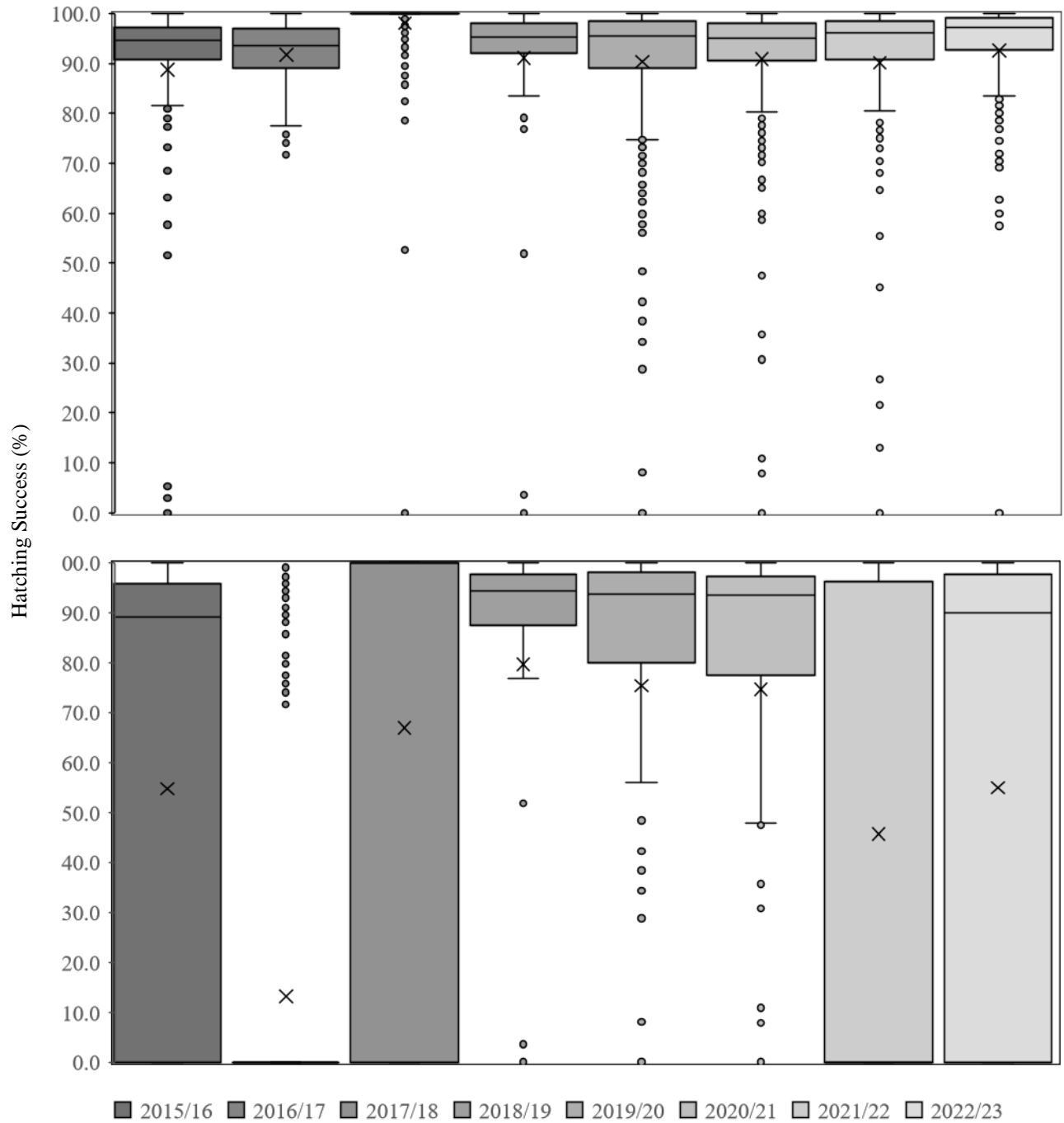


Figure A1: Green turtle hatching success per nesting season in Príncipe Island. The top panel corresponds to estimates of H% without the ‘lost nests’; the bottom panel represents the hatching success including ‘lost nests’ with H% = 0. Mean values are marked with an ‘X’. The box represents the hatching success range and dots represent outliers.

For a better understanding and representation of Praia Grande's data, hatching success was plotted in Figure S1. The top plot representing the hatching success excluding 'lost nests' and predated eggs, shows in general higher and more consistent hatching rates across all years compared to the bottom plot which includes 'lost nests'. The later exhibits more variability and lower median values. Outliers in both plots suggest that certain nests experience significantly lower hatching success due to various factors and that the graphs do not fit the data in the best way possible. The patterns indicate that some years consistently have high success rates while others show significant variability and lower success, pointing to changing conditions or interventions impacting hatching success.

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