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Nesting Behavior of Loggerhead Sea Turtle *Caretta caretta* in  
Boa Vista Island, Cape Verde: Nesting Frequency, Inter-Nesting  
Interval and Remigration Interval

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Maria Alice Radu MSc

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*Loggerhead turtle nesting at João Barrosa Beach. Photo: E. Davò, volunteer at Bios.CV.*

## Abstract

This study investigates the reproductive behavior of the Loggerhead sea turtles (*Caretta caretta*) nesting in Boa Vista Island, Cape Verde, focusing on three nesting parameters: Number of Nests (NN), Inter-Nesting Interval (INI) and Remigration Interval (RI). A database spanning across an 11-year period (2013-2023) and comprising of 30,957 observations of nesting activity from 21,580 unique tagged females was analyzed. This represents the first time-series dataset with >10 years of continuous data from Boa Vista Island, contributing to a better understanding of one of the most important Loggerhead rookeries in the world and of the endangered Northeast Atlantic sub-population.

Data analysis revealed a significant increase in the number of nesting females ( $R^2 = 0.47$ ,  $p = 0.019$ ) and in the number of nests ( $R^2 = 0.44$ ,  $p = 0.025$ ) over the years, with a strong correlation between the two ( $R^2 = 0.98$ ,  $p < 0.001$ ). Over the years, 11 females were recorded laying 5 nests within a single season, and 1 female was recorded nesting 6 times. An adjusted average NN based on these more frequently observed individuals ( $n = 12$ ) suggested a more realistic average NN of 4.11 per female/season, despite the majority of nesting turtles (82.21%) were recorded nesting only once, resulting in the overall average NN of 1.19 per female/season.

The most common inter-nesting intervals ranged between 7-14 days (21.61%) and 14-21 days (21.66%). Remarkably, a small percentage of nesting females (0.87%) exhibited an average INI between 1-7 days ( $1 < x \leq 7$ ) – an unusually short and infrequently documented pattern in the literature. The overall average INI adjusted for the more frequently observed nesting females ( $n = 12$ ) was 16.15 days, despite the majority of females (35.9%) presented an average INI >28 days – likely due to missing nesting events - resulting in a higher overall population average of 26.83 days.

The most common remigration intervals were 3 years (46.69%) and 2 years (29.83%). Interestingly, 3.09% of the nesting females nested in consecutive seasons, with some exhibiting this pattern in more than one nesting cycle. Additionally, 3 females were recorded nesting in 5 out of the 11 monitored seasons, and 1 individual was observed nesting in 6 seasons out of 11.

Overall, while a significant increase in nesting activity over the years was noted, a relevant part of the monitored females - 89.39% - was not observed returning in subsequent seasons. After accounting for the limitations of the monitoring program and the possibility that some turtles were missed, an alternative hypothesis emerged. Along with the consistently high proportion of newly tagged individuals over recaptured ones observed over the years, this may suggest a high turnover within the adult population and, therefore, a high mortality. Considering that on-land mortality in Cape Verde has declined as a result of the long-term conservation programs implemented over the last few decades, it is plausible that adult mortality is occurring at sea - particularly in foraging areas on the Northwest African coast, in countries such as Mauritania, where threats like bycatch and exploitation persist. These findings indicate the need for extending conservation efforts and funding to marine habitats, especially in the feeding grounds.

## Zusammenfassung

Diese Studie untersucht das Fortpflanzungsverhalten der Unechten Karettschildkröte (*Caretta caretta*), die auf der Insel Boa Vista, Kap Verde, nistet. Dabei konzentriert sich diese Studie auf drei Nistparameter: Number of Nests (NN), das Inter-Nesting Interval (INI) und die Remigration Interval (RI). Eine Datenbank, die sich über einen Zeitraum von 11 Jahren (2013-2023) erstreckt und 30.957 Beobachtungen der Nistaktivitäten von 21.580 markierten Weibchen umfasst, wurde analysiert. Dies ist der erste Zeitreihendatensatz mit mehr als 10 Jahren kontinuierlicher Daten von der Insel Boa Vista, der zu einem besseren Verständnis einer der wichtigsten Unechten Karettschildkröten-Kolonien der Welt und der gefährdeten Teilpopulation im Nordost-Atlantik beiträgt.

Die Datenanalyse ergab einen signifikanten Anstieg der Anzahl der nistenden Weibchen ( $R^2 = 0,47$ ,  $p = 0,019$ ) und der Anzahl der Nester ( $R^2 = 0,44$ ,  $p = 0,025$ ) im Laufe der Jahre, wobei eine starke Korrelation zwischen beiden besteht ( $R^2 = 0,98$ ,  $p < 0,001$ ). Im Laufe der Jahre wurden 11 Weibchen registriert, die in einer einzigen Saison 5 Nester legten, und 1 Weibchen, das 6 Mal nistete. Eine bereinigte durchschnittliche NN auf der Grundlage dieser häufiger beobachteten Individuen ( $n = 12$ ) ergab eine realistischere durchschnittliche NN von 4,11 pro Weibchen/Saison, obwohl die Mehrheit der nistenden Schildkröten (82,21 %) nur ein einziges Mal aufgezeichnet wurde, was zu einer durchschnittlichen NN von insgesamt 1,19 pro Weibchen/Saison führte.

Die häufigsten Inter-Nesting Intervals lagen zwischen 7-14 Tagen (21,61 %) und 14-21 Tagen (21,66 %). Bemerkenswert ist, dass ein kleiner Prozentsatz der nistenden Weibchen (0,87 %) ein durchschnittliches INI zwischen 1-7 Tagen ( $1 < x \leq 7$ ) aufwies - ein ungewöhnlich kurzes und in der Literatur selten dokumentiertes Muster. Der INI, der um die häufiger beobachteten nistenden Weibchen ( $n = 12$ ) bereinigte Gesamtdurchschnitt lag bei 16,15 Tagen, obwohl die Mehrheit der Weibchen (35,9 %) eine durchschnittliche INI - wahrscheinlich aufgrund fehlender Nestereignisse - von  $>28$  Tagen aufwies, was zu einem höheren Gesamtpopulationsdurchschnitt von 26,83 Tagen führte.

Die häufigsten Remigration Intervals waren 3 Jahre (46,69 %) und 2 Jahre (29,83 %). Interessanterweise nisteten 3,09 % der nistenden Weibchen in aufeinanderfolgenden Jahreszeiten, wobei einige dieses Muster in mehr als einem Nistzyklus aufwiesen. Darüber hinaus wurden 3 Weibchen in 5 der 11 überwachten Jahreszeiten beim Nisten beobachtet, und 1 Individuum wurde in 6 der 11 Jahreszeiten beim Nisten beobachtet.

Insgesamt wurde zwar eine deutliche Zunahme der Nistaktivität im Laufe der Jahre festgestellt, aber ein erheblicher Teil der überwachten Weibchen - 89,39 % - kehrte in den folgenden Jahren nicht zurück. Unter Berücksichtigung der Einschränkungen des Überwachungsprogramms und der Möglichkeit, dass einige Schildkröten übersehen wurden, ergab sich eine alternative Hypothese. Zusammen mit dem über die Jahre hinweg beobachteten konstant hohen Anteil neu markierter Individuen gegenüber wieder gefangenen, könnten diese Daten auf eine hohe Fluktuation innerhalb der erwachsenen Population und damit auf eine hohe Sterblichkeit hindeuten. In Anbetracht der Tatsache, dass die Sterblichkeit an Land auf den Kapverden infolge der langfristigen Schutzprogramme der letzten Jahrzehnte zurückgegangen ist, ist es plausibel, dass die Sterblichkeit der adulten Tiere auf See stattfindet - insbesondere in den Futtergebieten an der nordwestafrikanischen Küste, in Ländern wie Mauretanien, wo Gefahren wie Beifang und Ausbeutung fortbestehen. Diese Ergebnisse zeigen, dass die Schutzbemühungen und die Finanzierung auf marine Lebensräume ausgeweitet werden müssen, insbesondere auf die Futterplätze.

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# 1. Introduction

## 1.1. Biology and Ecology

The Loggerhead sea turtle (*Caretta caretta*) belonging to the family Cheloniidae is one of the seven species of sea turtles currently known. This large, hard-shelled, sea turtle can have a straight carapace length (SCL) ranging from 70 cm to 95 cm in its adult stage and can usually reach a weight between 80 kg and 200 kg, with regional and individual variation (Ernst & Lovich, 2009). It distinguishes from other species of marine turtles through the five vertebral scutes and five lateral scutes present on its carapace, through its reddish-brown color and through its big and disproportional head from which it derives its common name (Fig. 1). The lifespan of Loggerheads is long but complex estimated to be more than 50 years, with slow growth rates, high juvenile mortality and delayed sexual maturity reaching a reproductive age after 20-30 years (Dodd, 1988; Casale et al., 2011). Present in the Atlantic, Pacific, and Indian Oceans, this species is the most abundant in the subtropical and warm temperate regions of the ocean and has a complex lifecycle characterized by long migrations through entire ocean basins and different types of habitats (Bolten, 2003). It plays an important role in marine ecosystems contributing to maintaining the health of seagrass beds and coral reefs by grazing on seagrass and actively, intentionally, removing algae from coral reefs (Goatley et al., 2012). Loggerhead turtles are small ecosystems themselves, mobile islands hosting and transporting across the ocean epibionts such as barnacles, shrimps, algae and remoras that often cover the carapace of adults or live attached to them in a commensal symbiosis (Spotila, 2004). Acting both as predator and prey, Loggerheads occupy a significant place in the food web, and feed primarily on benthic invertebrates, such as crustaceans and mollusks, while maintaining opportunistic feeding habits depending on the diversity of local communities (Lazar et al., 2002). They forage both in open waters and in the nearshore areas in the tropical and temperate ocean basins (Spotila, 2004), while for reproduction they undergo long migrations to return to the nesting grounds, located primarily in subtropical and tropical coastal regions, often traveling thousands of kilometers between foraging and nesting sites (Bolten, 2003; Marcovaldi et al., 2010).

Loggerheads have a complex nervous system that enables navigations across vast distances in the open ocean and to specific geographic areas. Yet, the precise navigation systems guiding them in these long-distance reproductive migrations remain partially unknown and are subject of numerous studies and speculations (Lohmann et al., 2008). They have been hypothesized to rely - as other ocean migrants - on a combination of environmental cues, such as magnetic field and hydrodynamics (waves). These form a dual navigational system composed of two different mechanisms operating over different spatial scales that are thought to guide them through the ocean bringing them in proximity of their natal beach where they will reproduce. Afterwards, once they are near, the second mechanism is thought to supplement the first one and lead them to their final destination (Lohmann et al., 2008). There is evidence that the first mechanism is a magnetic map sense (Lohmann et al., 2004), while the second mechanism is hypothesized to be an olfactory sense that guides them once they are close to the target area (Lohmann et al., 2008).

In fact, sea turtles generically tend to exhibit natal homing to varying degrees and tend to return to their birthplace for reproducing (Bowen et al., 1993). This tendency seems to be driven by imprinting on environmental cues rather than by site-specific genetic programming (Bowen et al., 1989). However, while some exhibit a high nest-site fidelity returning to their exact natal beach for nesting, genetic studies revealed that others can occasionally shift to nearby beaches within the same region (Bowen, 2003; Miller et al., 2003).

Just as the other sea turtle species and most other reptiles, Loggerheads are an oviparous species that reproduces through the deposition of eggs in self-built subterranean nests (Deeming, 2004). Unlike mammals, female turtles do not experience reproductive senescence and can potentially continue nesting throughout their lifetime (Margaritoulis et al., 2020; Silva et al., 2022). However, reproductive migrations and egg production are highly energy-demanding, and most females do not undertake them every year, following rather a remigration interval (RI) of two to three years (Hatase & Tsukamoto, 2008; Hays, 2000).

After the long migrations to the nesting beaches during the breeding season, Loggerheads mate offshore, and females emerge on the nesting beach for the eggs' deposition (clutch size can vary between 60 to 120 eggs) multiple times during the same nesting season. Nesting females search for and carefully choose the site to dig their nests. They decide on the exact shape and depth of the nest chamber by digging it with their back flippers (Lutz et al., 2002). This phase can be crucial for later hatching success, since site-selection and nesting Behavior can determine the temperature in the nest by influencing factors such as the level of sun exposure over the nest, the water content in the sand, the heat conductivity or finally, the sand temperature due to depth (Marco et al., 2018). In fact, most turtles (Bull & Vogt, 1979) as well as many other reptiles (Ferguson, 1982) exhibit a temperature-dependent sex determination (TSD) and the temperature regime in the nest can heavily impact both embryonic development (Hendrickson, 1958) and hatchling characteristics and Behavior (Booth & Astill, 2001). In general, to optimize nesting success, Loggerheads need a sand temperature range that can support embryo development typically between 25°C and 33°C, while extreme temperatures outside this range can exhibit a reduced hatching success and an increased mortality rate (Hawkers et al., 2009). This complicates conservation efforts as artificial hatcheries may not always reflect natural incubation conditions, potentially skewing sex ratios (Robledo-Avila et al., 2023).

Loggerheads are a single species globally divided into 10 biologically defined Regional Management Units (RMUs) (Wallace et al. 2010), established based on the biology and geographic distribution of population segments, by integrating data from nesting sites, genetic analysis of mitochondrial and nuclear DNA, movement patterns and habitat use across different life stages (Casale & Marco, 2015). RMUs are functionally equivalent to the IUCN sub-populations and are meant to define geographic distributions of threats and population units in order to facilitate protection and provide guidance to marine planning initiative (Casale & Marco, 2015; Wallace et al. 2010).

One of these is the Northeast Atlantic (NEA) sub-population, the second largest nesting aggregation in the Atlantic Ocean (Monzón-Argüello et al., 2010). This sub-population can be found at the Cape Verde Islands and exhibits different genetical traits that distinguish it from other loggerhead populations (Monzón-Argüello et al., 2010). Although some loggerhead females may not be fully loyal to their birthplace, in the Northeast Atlantic sub-population nesting females show high site fidelity with no documented cases of individuals from Cape Verde nesting elsewhere, suggesting that this sub-population functions as a relatively closed genetic unit (Monzón-Argüello et al., 2010).

Overall, Loggerhead turtles are a fascinating species, yet with a very complex biological system to describe. Despite decades of research, understanding all aspects of their biology and their complete life cycle remain a challenge, as tracking sea turtles throughout their entire lifespan is not possible. Studying Loggerhead nesting populations is important for the conservation and management of this vulnerable species. Since the acquirement of all the necessary data is not possible, data collected through monitoring programs, although incomplete, are the best source to rely on.



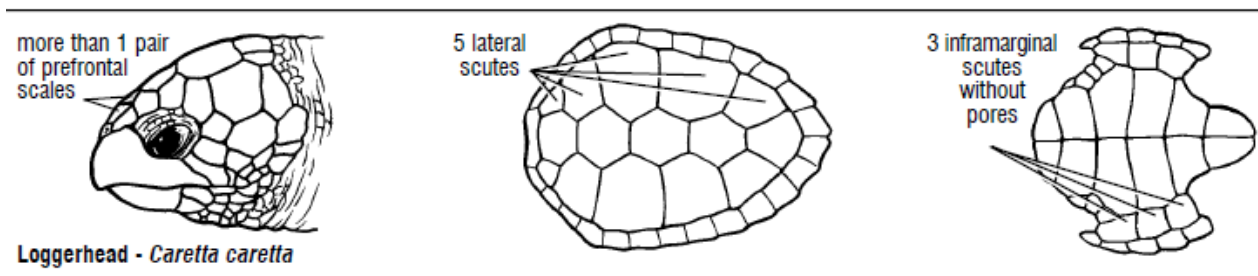


Figure 1: Species identification

Source: Wyneken, J. (2001). Species identification of sea turtles. In *The anatomy of sea turtles* (p. 4). NOAA Technical Memorandum NMFS-SEFSC-470. Public domain.

## 1.2. Aim of the Study

This study aims at conducting an intra-population analysis of the nesting Behavior of the Northeast Atlantic (NEA) sub-population of *Caretta caretta* over an 11-year period. Specifically, it seeks to analyze the reproductive patterns of the females belonging to this sub-population and investigates how frequently they lay nests within a single nesting season, the interval between nests, and the duration of their remigration cycles. By observing their nesting activity for 11 nesting seasons spanning from 2013 to 2023, this study aims to investigate the following three reproductive parameters:

- I. The nesting frequency, defined as the total **Number of Nests (NN)** laid by individual turtles within a single nesting season.
- II. The **Inter-Nesting Interval (INI)** or intra-seasonal nesting rate, described as the interval in days between consecutive nests laid by individual turtles within a nesting season.
- III. The **Remigration Interval (RI)** or reproduction interannual frequency, defined as the number of years between successive nesting seasons for individual turtles (Broderick et al., 2003).

In this study, nesting season (NS) defines the period ranging from June to October, corresponding to the reproductive period of Loggerheads in Cape Verde. Nesting activity typically begins in mid-June and extends until mid-October (Fig. 2), with very low activity in early June and in the second half of October, while peaks in the nesting activity are usually observed in August.

Average estimates of the parameters under examination have already been calculated in previous studies, based on a database including the nesting seasons from 2013 to 2018 (Martins et al., 2022b). A more detailed analysis of a larger database, including nesting seasons from 2013 to 2023, is required to refine these estimates and have a more precise overview of the nesting patterns of the sub-population (see paragraph 1.4.).

To analyze these parameters, this study investigates the nesting Behavior of the Northeast Atlantic sub-population of *Caretta caretta* nesting at João Barrosa Beach on the island of Boa Vista, one of the most relevant rogueries worldwide. This island hosts approximately 60% of the nesting activity of this population within just a few kilometers of sandy coastline (see 1.3). This aspect makes this sub-population very vulnerable to climate change and anthropogenic activity and classifies it as an endangered species according to the IUCN criteria (see paragraph 1.4.).

By analyzing these three parameters, this study seeks to extend our understanding regarding the reproductive strategies and adaptability of *Caretta caretta* in response to environmental and anthropogenic pressures. The findings may help to further develop targeted conservation programs and to ensure the long-term survival of this sub-population.

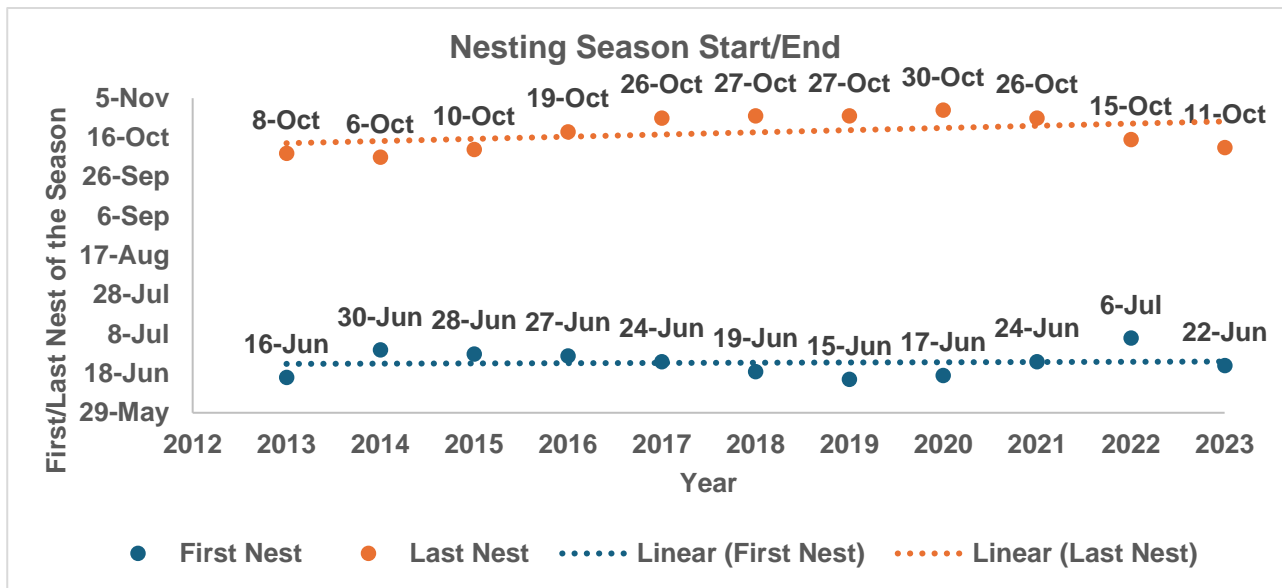


Figure 2: Beginning and end of nesting seasons at João Barrosa Beach

### 1.3. Research Site

This study has been carried out on the island of Boa Vista in the Republic of Cape Verde, more specifically at João Barrosa Beach (JB Beach) (Fig. 3). Cape Verde is an archipelago comprised of 10 major volcanic islands, of which 9 are inhabited, situated in the Northeast Atlantic about 500 km west of Senegal. Boa Vista, with its approximate surface area of 600 km<sup>2</sup> is the third-largest island in Cape Verde. The coastline can vary from urban to near-wilderness areas, with white sandy beaches along most of the perimeter - one of the factors which makes it the second-most popular island for tourism, alongside the well-developed infrastructure for international visitors and the luxury resorts.

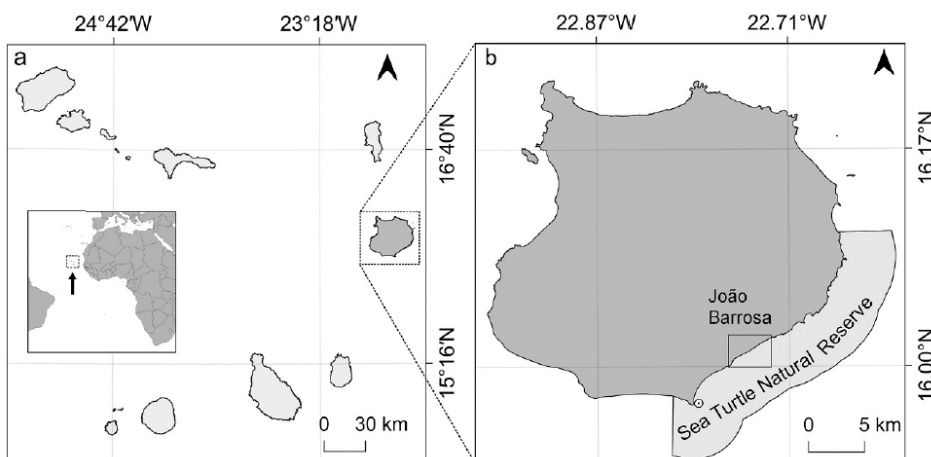


Figure 3: Map of Cape Verde, West Africa, and of Boa Vista Island

(A) Map of the Cape Verde islands, West Africa (inset map shows the location of the Cape Verdean archipelago off the coast of West Africa), and (B) map of Boa Vista (showed in dark grey inside dashed box in [A]). The location of the João Barrosa Beach is inside the frame. Light grey area shows the boundaries of the Sea Turtle Natural Reserve. Source: Martins et al., 2022

João Barrosa Beach, approximately 5 km long, is located in the south-east part of the island in a desert area shaped by the island's arid climate, with minimal vegetation adapted to its dry and saline conditions, such as small bushes of halophytic plants (Fig. 4). It is a distance away from one of the

few paved roads crossing the island, making this area even more isolated, away from any source of light pollution or anthropogenic disturbance. The area has been largely uninhabited for decades, since the few families abandoned the small fishing villages on the coast in the late 20<sup>th</sup> century. Human presence now is minimal, if excluding the seasonal mobile camp site of Bios CV and the tourists reaching the place by day tours, mainly for turtle watching. All these factors contribute to maintaining the pristine environment of the area and help preserving this key nesting site for sea turtles.



Figure 4: Aerial view of João Barrosa Beach with visible turtle tracks

Source: Drone-captured aerial photograph by E. Davò, volunteer at Bios.CV, nesting season 2024

Cape Verde Islands host the second largest nesting aggregation in the Atlantic Ocean of the globally vulnerable and locally endangered Loggerhead sea turtles (IUCN 2015) and represent the only major rookery in Western Africa, between South Africa and western Europe (Monzón-Argüello et al., 2010). While many of the ten Regional Management Units (RMU), or sub-populations, defined for the Loggerhead sea turtle contain numerous nesting sites (Wallace et al., 2010) within the Northeast Atlantic RMU, Cape Verde is the most important nesting site for this species (Fig. 5) (Casale & Marco, 2015).

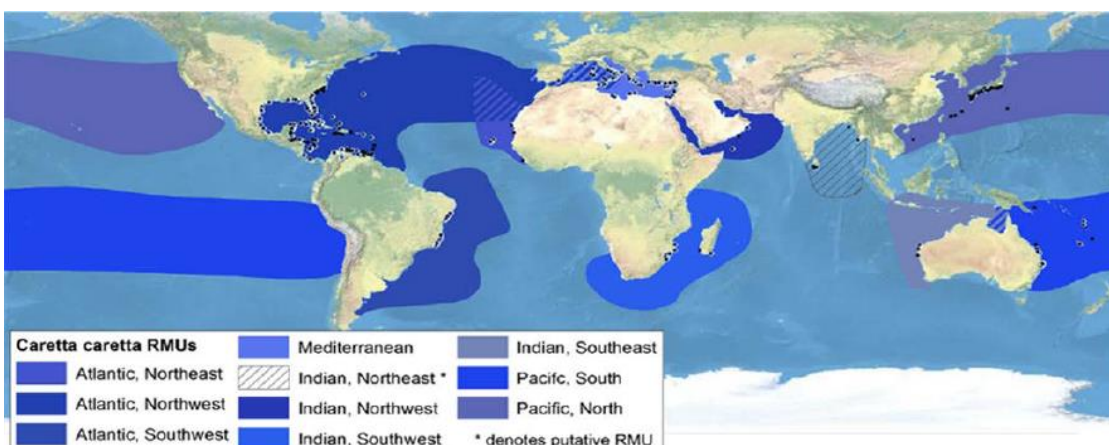


Figure 5: Global map of the distribution of the 10 IUCN Loggerhead sub-populations (RMUs)

Source: Wallace et al. 2010

Although nesting activity is recorded for most of the islands in the archipelago, the vast majority occurs in Boa Vista, hosting 90% of the activity in the archipelago (Marco et al., 2008) and around

60% of the total nesting activity of the endangered Northeast Atlantic sub-population (Marco et al., 2012). Within the island, more than 50% of the total nesting activity of this RMU is supported by the Sea Turtle Natural Reserve on the south-east coast (Fig. 3), covering the area of the three main beaches of João Barrosa, Ervatão and Calheta Lajedo Teixeira. Of these, João Barrosa alone hosts approximately 25% of the nesting activity in the Natural Reserve (Marco et al., 2012).

#### 1.4. Significance of the Research

The Northeast Atlantic sub-population has been identified as a separate genetic population and reproductively isolated from all other Loggerhead populations (Monzón-Argüello et al., 2010). The Cape Verde archipelago is the main, if not the only, rookery for this sub-population (Marco et al., 2012). This factor qualifies this sub-population for the category “Endangered”, according to the IUCN Red List criterion B2 sub-criteria (a) and (b) (Casale & Marco, 2015). This criterion is considering the relatively small area of occupancy<sup>1</sup> (AOO) with a limited number of nesting locations and the continuous anthropogenic pressure this area is subjected to. In fact, the main rookery at Cape Verde is suffering not only from habitat degradation and rising sea levels due to climate change, but also from a continuous anthropogenic pressure, causing a decline in habitat area by extension and quality (Casale & Marco, 2015). In this rookery, females nest principally on small beaches across the archipelago (Marco et al., 2012), with >85% of the nesting activity occurring at beaches with low elevation vulnerable to tides (Ferreira-Veiga, 2018) and with a high number of tourists (Marco et al., 2011). Natural and anthropogenic factors include tidal inundation, high levels of predation by ghost crabs (*Ocypode cursor*) and crows, sand removal, pollution and tourism-associated coastal development (Sarmiento-Ramírez et al., 2010; Marco et al., 2011, 2015, 2018, 2021; Martins et al., 2021). Organized turtle-watching activities by tourist have also developed rapidly over the last few decades, initially with <500 tourists in early 2000’, and >10,000 per year in 2018 and 2019, potentially altering nesting Behavior, especially camouflaging, if protocols of turtle watching are not being implemented correctly (Marco et al., 2021). Beside these, the Cape Verdean turtle aggregation historically faced serious conservation threats, derived from a significant illegal harvest of eggs and adult females on the beaches, and the catch of both males and females in nearby waters due to harvest or by-catch in fisheries (López-Jurado et al. 2000; Marco et al. 2008). In 2007, it was estimated that around 1,150 females were captured in the archipelago (Marco et al. 2008) for their meat. For all the reasons mentioned, Cape Verdean turtle aggregation constitutes a key conservation unit that deserves attention, monitoring and conservation efforts.

The criterion C of the IUCN Red List was not applied since with 8,900 estimated nesting females in 2012 (Marco et al., 2012), the population was considered relatively stable. Other criteria, such as criterion A, could not be applied due to the lack of time series datasets with ≥10 years of data representing the sub-population nesting activity (Casale & Marco, 2015). The dataset analyzed in the present study represents, in fact, the first time-series dataset with >10 years of continuous data for this RMU from Boa Vista Island<sup>2</sup>. While there is ongoing monitoring by other associations as well and published research on Loggerhead turtles nesting in Cape Verde, there is still a lack of publicly accessible long-term time-series datasets specifically for Boa Vista Island.

Furthermore, although the parameters studied in the present research have been also determined in other Loggerhead sub-populations, little is known about the nesting patterns of the Northeast

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<sup>1</sup> AOO is identified with the nesting beach habitat. The total length of known Loggerhead nesting beaches in the Cape Verde Archipelago is 212 km (Casale & Marco, 2015).

<sup>2</sup> The first 10-year dataset of Loggerhead turtles nesting activities on Sal, another island in the Cape Verdean archipelago, has been analyzed in “Laloë et al., 2019”, while previously no other >10-year dataset was available (Casale & Marco 2015).

Atlantic RMU nesting in Cape Verde. A study conducted in Northern Cyprus for two years, from 1993 to 1995, involving 99 tagged females of *Caretta caretta* - the most comprehensive study conducted in the Mediterranean at that time - reported an average of 1.6 nests per season, with an inter-nesting interval of 13.5 days and a remigration interval of 2 and 3 years, although some turtles were recorded nesting in consecutive seasons (Broderick, 1999). Another study, conducted in northeastern Brazil and involving 10 satellite-tracked Loggerhead females belonging to the Southwestern Atlantic sub-population, reported different remigration intervals of 2 or 3 years, while inter-nesting intervals and the number of nests were not determined (Marcovaldi et al., 2010). Regarding the Atlantic Northwest RMU, a study conducted in Mexico between 1995 and 2018 investigated the remigration interval for 926 tagged Loggerhead females revealing a peak at 726 days with a 12-day inter-nesting interval (González et al., 2020).

In contrast, for the Northeast Atlantic sub-population, publications directly addressing the nesting parameters analyzed in this research remain scarce. In a study from 2012 on Boa Vista Island (Marco et al., 2012), the authors assume a remigration interval of 2.4 years based on previous research (Varo-Cruz et al., 2007). In this last paper, field work conducted on Boa Vista Island between 1998 and 2002 led to the estimation of this remigration interval by investigating the nesting patterns of 252 recaptured Loggerhead females (Varo-Cruz et al., 2007). In another paper from 2021, the first comprehensive study of Loggerhead turtles nesting in Maio - another island of the Cape Verdean archipelago, hosting high nesting activity – the authors estimated an approximate number of nesting females per year for the period 2016-2019 based on the assumption that females produce 3-5 clutches per season (Patiño-Martínez et al., 2021). This assumption is based on the research conducted on Boa Vista Island between 1998 and 2004, the first study made on the South-East coast to characterize the population nesting on the three beaches of Calheta, Ervatão and Ponta Cosme (Varo-Cruz, 2010). In this study, among the 3,920 turtles tagged in Boa Vista and 273 tagged in Sal Island the most common remigration interval was 2 years followed by a 3-year interval; breeding annually was affirmed to be unusual and rare in Loggerhead females due to the high energetic cost of reproduction and migration (Varo-Cruz, 2010). Average number of nests per season was 1.4 and 1.6 nests/female with an average inter-nesting interval of  $15.0 \pm 1.8$  days.

The most recent study was published in 2022, where the effect of body size on the long-term reproductive output of NEA Loggerhead turtles was investigated by analyzing a database spanning from 2013 to 2018 (Martins et al., 2022b). Here, an average RI of 3.12 years was calculated for 449 tagged females, while an average INI of 14.83 days was calculated for 1052 females monitored while nesting at JB Beach, with an average NN of 1.44 nests/female in a season. However, while average values of these nesting parameters have already been calculated, a more detailed analysis of a larger database - the first one with >10 years of continuous data from Boa Vista Island - including nesting seasons from 2013 to 2023 is required to refine these estimates and have a more precise overview of the sub-population's nesting patterns and their variation over time.

Investigating nesting frequencies and parameters such as remigration and inter-nesting intervals helps in understanding the reproductive ecology of sea turtles, as it can provide insights into reproductive cycles and population dynamics. The remigration interval, for instance, since it reflects the time that individuals require to accumulate enough energy reserves to undergo a full reproductive cycle, can provide information about females' reproductive physiology: it helps estimating the duration of ovulation cycles and of ovarian follicle development, as well as the duration of vitellogenesis (yolk formation process during eggs development). Variation in remigration intervals could also act as indicators of population's health and environmental pressures, since external factors such as climate change and ocean productivity could affect foraging success and, therefore,

impact their reproductive ability. Shorter intervals could, for example, indicate favorable conditions such as higher availability of food, while longer intervals might suggest changes or degradation in foraging habitats. Similarly, variations in RI can help to understand population viability with stable or decreasing RI potentially indicating a healthy population, whereas increasing RI averages suggest stress due to environmental or anthropogenic pressures affecting reproductive success. Therefore, long-term monitoring and tracking such nesting parameters over multiple nesting seasons can help to detect any variation in population's reproductive health and structure and enable a timely and adequate response through the adjustment of conservation plans.

## **2. Methodology & Data**

### **2.1. Data Collection & Database**

Data about nesting turtles have been continuously collected by the non-governmental organization Bios CV for 11 nesting seasons ranging from 2013 until 2023, forming a database with more than 30,000 observations of nesting activities. Throughout the eleven seasons, JB Beach has been monitored daily from the 1<sup>st</sup> of June until the 31<sup>st</sup> of October. This period covered the nesting season of Loggerhead turtles in Cape Verde - usually starting around mid-June and ending around mid-October - plus two additional weeks at the beginning and at the end to enable the record of eventual early and late nests. To ensure a standardized monitoring effort through the single nesting season and through the years, a stable number of teams and monitors has been involved throughout the entire period. When necessary, this number has been adjusted to the amount of nesting activity during high-activity nesting seasons. Moreover, established protocols have been applied and the same data collection methodology has been followed throughout the entire eleven-year period to ensure continuity. During the covered period, every night, when females emerged on the beach for nesting, trained teams composed of at least one experienced monitor supported by two to three volunteers conducted the monitoring activity. Beach patrolling started at 20:00 h and lasted until approximately 8:00 h the next morning, and was divided into two patrol shifts, from 20:00 h to 02:00 h and from 02:00 h to 08:00 h to reduce error due to fatigue. JB Beach, extending for 5 km in total, was divided into three sectors – North, South, and End South – to reduce the distance covered by each team and ensure a more accurate data collection. Therefore, every night, 6 teams in total were involved in the monitoring activity, while factors such as beach sector, shift schedule and team members were rotated every night and assigned randomly, to minimize errors due to fatigue and avoid inequalities. When encountering a female, the team hid in the dark or behind the turtle, to minimize interference and disturbance during the crawl and oviposition and to observe her Behavior. Only when the female finished laying eggs, or while camouflaging the nest or crawling back to sea, biometric data were collected. The nesting event, the date and the location of the nest, if laid, were registered, and the female identity was checked with an Avid Mini Tracker III scanner for the presence of a Passive Integrated Transponder (PIT) tag in the frontal flippers and neck area. Untagged females were tagged with an Avid FriendChip PIT tag in the right-frontal flipper, between the second and the third scale according to the Cabo Verde tagging protocol (Marco et al., 2012b) and registered as a “new” individual. If a PIT tag was detected, its code was recorded and the female marked as “re-captured”. Ultimately, other biometric data such as two measures of the curved carapace length (CCLmin and CCLmax) and the width of the carapace (CCW) were measured with a flexible measuring tape and eventual presence of abnormalities, amputations, and epibionts were recorded (Annex 4). During the arrival at the beach and the crawl back to the sea, females leave tracks in the sand that allow the monitors to assess whether the nesting activity resulted in eggs deposition or whether the female abandoned before oviposition. These tracks were assessed and counted during the early morning inspection, starting at 06:00 h, when the sun arose and the visibility increased, to



account for the total nesting activity that had happened and to record all the nests laid during the previous night. In this way, even in high-activity nights, a fairly accurate total number of nests was recorded, although monitoring all the nesting females arriving during the night hours was not possible. Morning inspections have been continuously carried out and periods when surveying was absent for a day or more have not occurred during the monitoring program. Overall, the monitoring and the data collection process have been carried out with respect and special care, to minimize the impact of the monitors' presence and to avoid disturbing females or altering their nesting Behavior. Stay out of the turtles' sight while emerging and searching for a nesting location, minimize working time and turtle manipulation and always use red light were some of the most important rules to observe.

Only some of the biometric data and the data inherent to the nesting activity that have been collected were used in this study. Four variables have been included in the dataset for analysis: the date of the nesting activity observed, the number of PIT tag identifying the turtle, the oviposition if happened (Nest "Yes", "No", or "Doubt"), and whether the female was a newly tagged individual or a re-capture (Re-capture "Yes" or "No"). This database enabled the analysis of the three parameters: the Number of Nests (NN), the Inter-Nesting Interval (INI) and the Remigration Interval (RI).

## 2.2. Data Analysis

To quantify the three main parameters under observation - namely the Number of Nests (NN), the Inter-Nesting Interval (INI) and the Remigration Interval (RI) – describing the nesting activity of *Caretta caretta* at João Barrosa Beach over an 11-year period (2013–2023), the database resulting from the monitoring activities has been analyzed. The data analysis was conducted using Microsoft Excel, following a structured approach to investigate the cleaned dataset containing 30,957 observations of nesting activities.

Before analyzing the core parameters, an initial exploratory analysis was conducted to describe the population structure and nesting trends over the years. Firstly, the total number of females tagged was calculated by identifying unique PIT tags in the dataset using the function "Remove Duplicates" in Excel. This was done both across the entire monitoring period and for individual nesting seasons to calculate the total number of nesting females per year and detect possible emerging trends over the years. This approach provided an approximate estimation of the population utilizing the beach annually and cumulatively. Secondly, a similar approach was used to quantify the total number of nests laid, both across the entire period and in individual nesting seasons. The total number of nests recorded each year was determined by filtering observations labelled as "Nest: Yes" and summing these values using Pivot Tables. A linear regression analysis was then performed to describe the trend followed by both the number of females and nests over time and verify whether that was statistically significant. Lastly, using Pivot Tables and COUNTIF formulas, the proportion of newly tagged individuals and the recaptured ones was determined annually to investigate whether the same females were returning to nest or whether new juveniles were being recruited into the population. Together, these metrics allowed the assessment of population density and variation over time while providing a comprehensive overview of the nesting activity and trends at the study site, serving as the foundation for further analyzes.

To investigate the first nesting parameters, the Number of Nests (NN) or nesting frequency, the total number of nests per individual turtle within a nesting season was calculated, followed by the percentage of females that nested between one and two times, two and three, or more times within a season using the COUNTIF function and Pivot Tables. To do so, firstly, all nesting events marked as "Yes" in the "Nest" column were filtered out, ensuring that only confirmed nesting events were

included in the analysis, and then counted season by season for each unique PIT tag. The average number of nests per season for individual turtles was determined. Females were then classified into different nesting frequency categories (e.g., turtles laying between one and two nests, two and three, three and four nests, etc. per season), and a population-wide average was computed. A further step involved filtering the dataset to identify only these individuals with particularly high numbers of nests per season, and a second average was calculated, to assess a more realistic average NN and investigate females' nesting potential. Probably, this second average NN would have been the value obtained by analyzing the entire database, if we were able to monitor all the nesting events happening in JB.

Furthermore, following the same approach adopted for the first analysis, a secondary analysis was conducted by including all recorded nesting activities, regardless of whether oviposition occurred or not (i.e., also including entries marked as "No" and "Doubt" in the "Nest" column). This approach allowed for a broader perspective on the nesting potential of Loggerhead turtles in this sub-population and accounted for the fact that some turtles may attempt to nest multiple times before successfully laying eggs.

To analyze the second nesting parameter, the Inter-Nesting Interval (INI), defined as the interval in days between two consecutive nests laid by the same individual within a nesting season, only individuals with at least two nests in a single season were considered. Using Pivot Tables and MIN/MAX functions, the earliest and latest nests for each individual in a given season were identified and the difference in days between consecutive nests was computed using date subtraction in Excel. IF and AVERAGEIFS functions were applied to calculate individual average INI while excluding intervals exceeding 180 days. To identify nesting patterns and observe nesting frequency trends, individual turtles were grouped into different interval categories (e.g., 7–14 days, 14–21 days, etc.) according to their individual average INI values, percentages have been calculated and a population-wide average INI was computed. An extra category was introduced for INI = 1 day to check for potential errors in data collection.

A refined analysis was then performed focusing on these individuals that exhibited the highest number of nests in a season to determine a more representative INI for the sub-population. This revised average INI, although including the minority of the cases, it may still be a better description of the nesting potential of Loggerhead females - again, it could be the value obtained from the analysis of the entire database and closer to reality as it was hypothetically possible to monitor all the nesting events happening on the beach.

Additionally, in line with the previous approach and applying the same methodology, a second extended analysis was conducted, considering all recorded returns, including failed nesting attempts or false crawls, instead of only oviposition events. This metric referred to as the Inter-Migration Interval (IMI) offered a broader perspective on how frequently turtles emerged on the beach, regardless of whether they successfully laid a nest or not, to explore the full nesting potential of the population.

For the analysis of the last nesting parameter, the Remigration Interval (RI), defined as the number of years between successive nesting seasons of the same individual, only a subset of the dataset was used. The analysis focused on turtles that had been recorded nesting in at least two separate seasons within the 11-year period. The COUNTIF function and Pivot Tables were used to identify each individual's first and subsequent nesting years and the interval between them was calculated. Afterwards, the single intervals between two consecutive nesting seasons of the same individual – and not the average RI per individual - were categorized into common remigration intervals (e.g.,



two, three, four years, etc.) to analyze the frequency distribution of remigration intervals and to determine how many turtles returned after one, two, three, or more years. Following this approach, turtles returning in multiple nesting seasons with different RIs were accounted more than once. In this way, it was possible to assess the most common RI patterns among females in the sub-population, ensuring that individual averages were not skewed by gaps in data or missed recordings. To obtain a representative estimate of the population's remigration Behavior, the weighted mean RI was computed by multiplying the number of cases for each RI category (e.g., 1-year, 2-year, 3-year intervals) and by calculating an average.

A separate analysis was conducted to investigate whether individual turtles consistently followed the same remigration pattern across multiple seasons. To do so, using a Pivot Table each PIT tag was analyzed to determine how many times the individual repeatedly exhibited the same RI over different nesting seasons. The individuals returning more often and presenting the same RI values over time were used to assess whether remigration Behavior tended to be consistent within the same individual or varied across different seasons.

Also for this parameter, a second analysis was performed to incorporate all the recorded emergences onto the beach - and not only the confirmed nests - to evaluate females' nesting potential and account for the possibility that, even though the nesting attempt in JB was unsuccessful according to our data, they might still have nested in other beaches or that the oviposition in JB was simply missed out.

Ultimately, a key challenge in the analysis was addressing duplicate values, instances where the same turtle was recorded twice on the same date. Several factors could explain these occurrences. One possibility is the documentation of false crawls, when a turtle emerged multiple times in a single night, unsuccessfully attempting to nest. In this case, the double entries in the "Nest" column were recorded as "No" & "No", if no oviposition occurred, or "No" & "Yes", if eventually the turtle successfully nested on a second attempt (Tab. 1). Another explanation involves errors in data collection, when duplicate records were marked as "Yes" & "Yes" in the "Nest" column (Tab. 1): this would suggest that two nests on the same night were laid by the same turtle - an unlikely biological occurrence - indicating probable mistakes in data collection or data transcription.

Table 1: Example of duplicate values: a possible false crawl (in green) and an error in data collection (in red)

	A	B	C	D	E	F	G	H
1	Datos de N2K y TF de 2016 a 2020 y BIOS de 2013 a 2022 y N2K de 2005 y 2007	BEACH	DATE	RE-CAPTURE	PIT TAG	NEST	NEST INDICATOR	YEAR
3848	BIOS.CV	J.B.	16/07/2017	No	977200009206278	No	0	2017
3881	BIOS.CV	J.B.	18/07/2017	Yes	977200009206278	Yes	1	2017
3882	BIOS.CV	J.B.	18/07/2017	Yes	977200009206278	Yes	1	2017
4281	BIOS.CV	J.B.	03/08/2017	Yes	977200009206278	Yes	1	2017
4294	BIOS.CV	J.B.	03/08/2017	Yes	977200009206278	No	0	2017

These duplicate values (n=277, of which 105 marked as "Yes" & "Yes" in the "Nest" column) were carefully reviewed and excluded from the Number of Nests and the Inter-Nesting Interval analyzes via Pivot Tables. However, for IMI (Inter-Migration Interval, considering all returns), an adjustment was made to account for these cases separately, ensuring they were not mistakenly included as separate observations.

By employing a combination of Pivot Tables, COUNTIF and AVERAGEIF formulas and data filtering techniques, this analytical approach allowed for a comprehensive assessment of the nesting

Behavior of *Caretta caretta* in João Barrosa Beach, while aiming at minimizing errors in data collection.

### 3. Results

#### 3.1. Results of Data Collection

The database resulting from the 11-year monitoring program implemented by Bios CV, contains a total of 30,957 observations of nesting activities recorded at JB Beach between June 2013 and October 2023. It contains data about the date of the nesting activity, the PIT tag number identifying the turtle, the oviposition if happened (Nest “Yes”, “No”, or “Doubt”), and whether the female was a newly tagged individual or a re-capture (Re-capture “Yes” or “No”) (Tab. 2).

Table 2: Sample of the database under analysis

	A	B	C	D	E	F	G	H
	Association	BEACH	DATE	RE-CAPTURE	PIT TAG	NEST	NEST INDICATOR	YEAR
1								
2	BIOS.CV	J.B.	16/06/2013	Yes	133332235A	Doubt	#N/A	2013
3	BIOS.CV	J.B.	21/06/2013	Yes	977200007756020	Yes	1	2013
4	BIOS.CV	J.B.	21/06/2013	No	977200008491040	Yes	1	2013
5	BIOS.CV	J.B.	21/06/2013	Yes	132836127A	No	0	2013
6	BIOS.CV	J.B.	22/06/2013	Yes	132855374A	Yes	1	2013
7	BIOS.CV	J.B.	22/06/2013	Yes	132924224A	Yes	1	2013
8	BIOS.CV	J.B.	22/06/2013	Yes	125461617A	No	0	2013
9	BIOS.CV	J.B.	23/06/2013	Yes	137557254A	Yes	1	2013
10	BIOS.CV	J.B.	24/06/2013	No	977200008492633	Yes	1	2013

The database has been analyzed in Excel for preliminary statistics to assess the general status of the nesting activity recorded in these years and to have an overview of the female population monitored. As showed in Table 3, a total of 30,680 observations have been used for further statistics – 277 observations have been removed since they were recorded twice. These “duplicate values” are nesting events recorded twice in the same day, due to several reasons. It might have happened either due to the change in patrolling team, due to double monitoring of the same turtle by the same team, or an error in data transcription from the working sheets to the digital database, or, finally, due to multiple crawls of the female in the same night<sup>3</sup>. Since the exact time of the encounter was not recorded in the database, determining a specific explanation for the duplicate values is not possible.

A total of 21,580 females were tagged during the entire monitoring program. This number, far away from representing the exact size of the female NEA population nesting in JB Beach, is still a valid approximation of the nesting activity happening in this area and of the population trends over the years. Of these, 19,462 are the nesting females that laid at least one nest over the entire period. The remaining 2,118 turtles emerged on the beach without recorded oviposition. A total number of 25,985 nests (entries marked as “Yes” in the “Nest” column) have been counted at JB Beach over the time period. Of these, 105 entries were duplicate values of nests, recorded twice in the same day, most likely due to errors in data collection or transcription, since it is biologically unlikely that turtles lay

<sup>3</sup> Females can emerge onto the beach multiple times during the same night, if the oviposition does not happen at the first time (“False crawl”). This could be due to disturbance or lack of an adequate location for a nest. In this case, the same turtle can be recorded twice in the database.

two nests within the same day. Without these duplicate values, a total of 25,880 nests were used for further statistical analysis. Ultimately, 176 observations in the database are representing nesting activities for which a clear assessment of the happened oviposition was not possible (therefore marked as “Doubt” in the “Nest” column). Overall, the database described above was used for the analysis of the three parameters.

Table 3: Overview of the database

Database in Summary, 2013-2023	
Numbers	Definition
30,957	Total Observations
277	Duplicate Values (nesting events recorded twice in the same day)
30,680	Total Observations, without 277 duplicate values (cleaned number used for statistics)
21,580	Total Tagged Females in the Population
19,462	Total of Nesting Females (females that laid at least one nest)
2,118	Turtles Never Nesting (females emerging and never laying eggs)
25,985	Total Number Nests (“NEST YES”), including 105 duplicate values
105	Duplicate Values (nests of same turtle recorded twice in the same day = Error)
25,880	Total Number Nests (“NEST YES”), without 105 duplicate values (cleaned number used for statistics)
176	Nests marked as “DOUBT” (when not possible to assess whether turtle laid the eggs or not)

To investigate the trend of the nesting activity over the years, the number of nesting females and the number of nests recorded in JB Beach each year have been analyzed. A linear regression analysis revealed that over the 11-year study period, the number of *Caretta caretta* females nesting at JB Beach significantly increased ( $y = 412.78x - 830,795$ ,  $R^2 = 0.47$ ,  $p\text{-value} = 0.019$ ) indicating a positive temporal trend, however, with substantial year to year variations (Fig. 6).

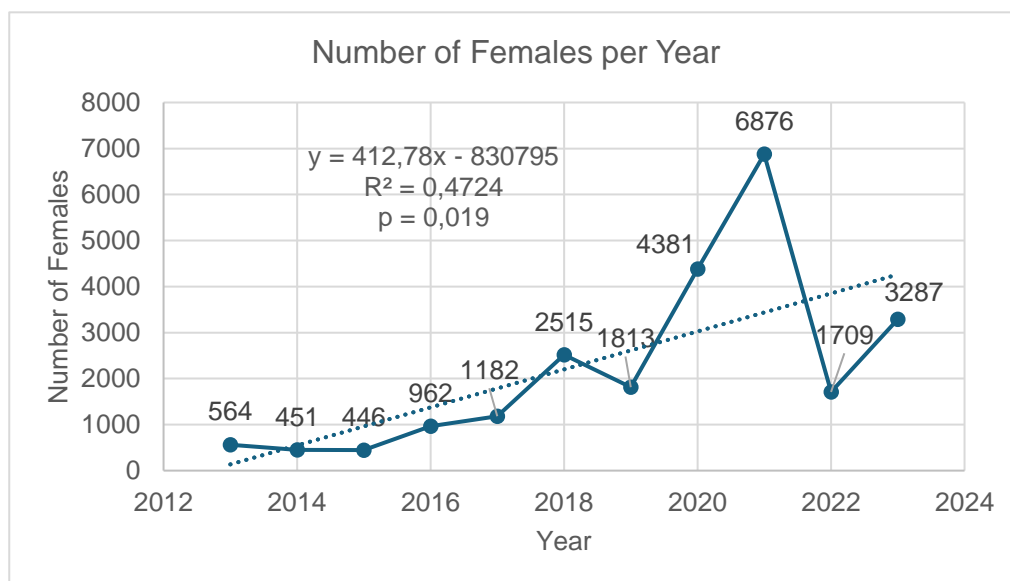


Figure 6: Number of females per year

Linear regression of the number of females recorded at João Barrosa Beach from 2013 to 2023. The trend shows a statistically significant increase over time ( $y = 412.78x - 830,795$ ,  $R^2 = 0.47$ ,  $p\text{-value} = 0.019$ ).

The lowest number recorded was in 2015, with 446 individuals, while the highest in 2021 with 6,876 individuals monitored, accounting for a total of 24,186 turtles that visited JB Beach over the 11-years period. The data highlighted interannual variability where notable peaks, such as those registered in 2018 and 2021, were followed by declines in the subsequent years (2019 and 2022). This fluctuation might reflect a combination of biological, environmental, and anthropogenic factors - such as a decrease in fishing activities during the pandemic for example - influencing nesting Behavior and population dynamics.

The number of nests recorded at JB Beach is strongly correlated to the number of females ( $y = 1.09x - 36.95$ ,  $R^2 = 0.98$ ,  $p\text{-value} = 2.36E-09$ ) (Annex 1). A linear regression analysis revealed a statistically significant increase in the number of nests over the years ( $y = 438.58x - 882,705$ ,  $R^2 = 0.44$ ,  $p\text{-value} = 0.025$ ), indicating a positive trend consistent with the increase observed in the number of females. A total of 25,580 nests have been recorded over the 11-years period with an average of 2,352.7 nests per year. The lowest number of nests recorded was in 2015 with 477 nests while the highest in 2021 with 7,681 nests (Fig. 7). Also in this case, data reflected an interannual variability where the peaks registered in 2018 and 2021 have been followed by declines in the subsequent years, in 2019 and 2022.

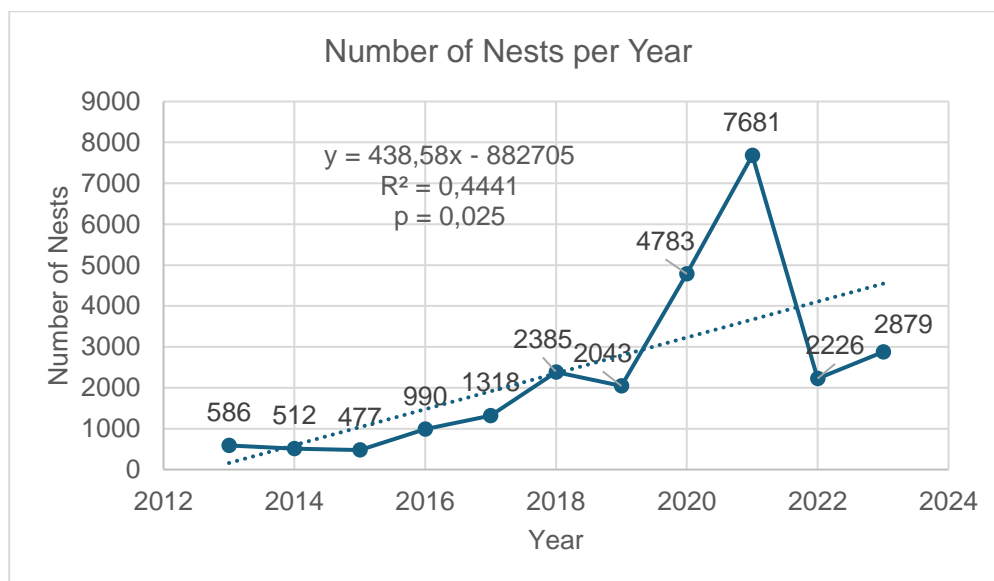


Figure 7: Number of nests per year

Linear regression of the number of nests recorded at João Barrosa Beach from 2013 to 2023. The trend shows a statistically significant increase over time ( $y = 438.58x - 882,705$ ,  $R^2 = 0.44$ ,  $p\text{-value} = 0.025$ ), consistent with the increase observed in the number of females.

To investigate the turnover in the population and to explain the increase in the number of nesting turtles, the ratio between the new-tagged individuals and the recaptures has been calculated. The results showed that the ratio remained fairly stable throughout the period with a dominance of newly captured individuals over the recaptured ones (Fig. 8). In 2013 and 2015, one and three cases, respectively, have been recorded as “NA”, probably due to the impossibility of reading the PIT tag at the moment of the observation. Therefore, it was impossible to classify the individual either as new or recaptured; these values were excluded from the total percentages for the years 2013 and 2015.

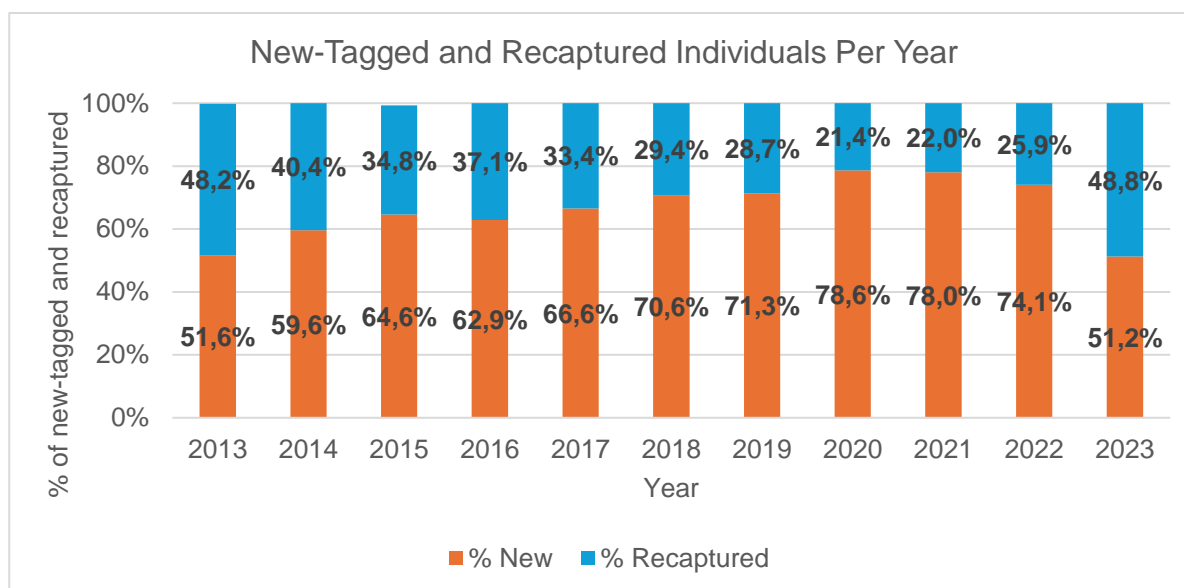


Figure 8: Ratio of new-tagged and recaptured individuals per year

Of the 21,580 females tagged in total, only about 20% have been observed returning to JB Beach over the entire 11-year period to lay more than one nest. In fact, for 69.53%<sup>4</sup> of the females corresponding to 15,005 individuals, only one nest has been recorded during the entire period (Fig. 9), while only 4,457 turtles have been observed nesting at least a second time.

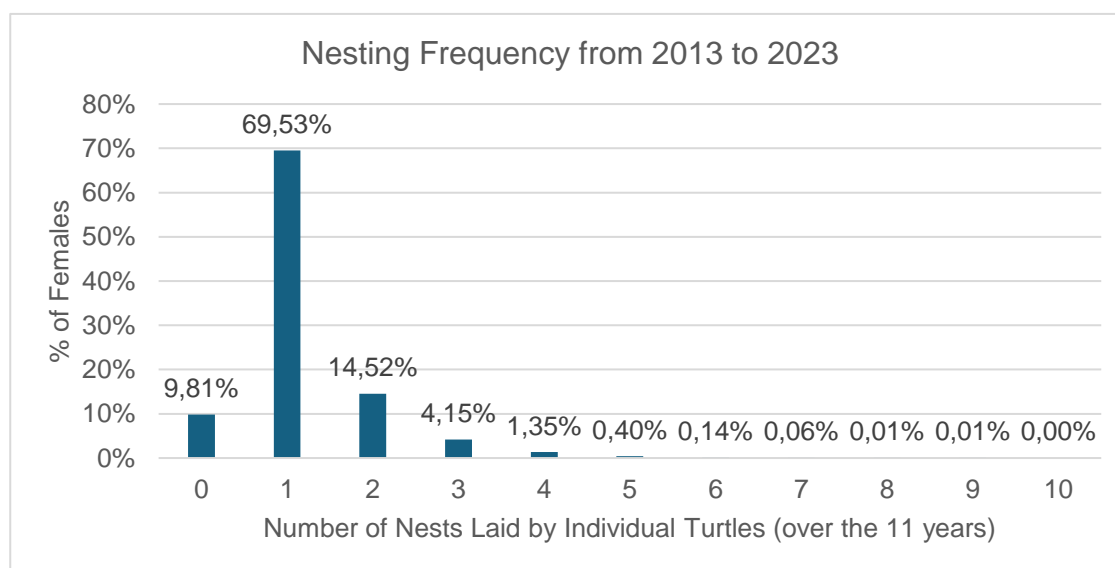


Figure 9: Number of nests laid by individual turtles over the 11 years

In the database, are recorded only three females with eight nests and two females with nine nests over the entire period (Tab. 4).

<sup>4</sup> In this thesis, percentages in graphs use a comma (e.g., 69,53%) as a decimal separator due to formatting constraints in Excel. However, in the main text, percentages follow the standard UK format with a decimal point (e.g., 69.53%).

Table 4: Special cases of females that have been recorded while nesting for eight or nine times over the entire period

Count of NEST PIT TAG	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	Grand Total
941000022739240						1		3		4		8
977200008331463		3			5							8
977200008491441	3				3			2				8
977200007390013	1		2		1		1	2		2		9
152109661A					3		4		2			9

After considering solely the nesting events that concluded with an oviposition, therefore only the times when the individuals effectively laid a nest ("Nest" marked as "Yes"), a second analysis has been conducted including all the nesting events to determine whether individuals returned more frequently but did not lay a nest. The trend of the migration frequency followed the one of the nesting frequency, with 73.5% of the females that have been observed coming only once (Fig. 10). Only 3,657 and 1,181 turtles, respectively, have been monitored a second and a third time.

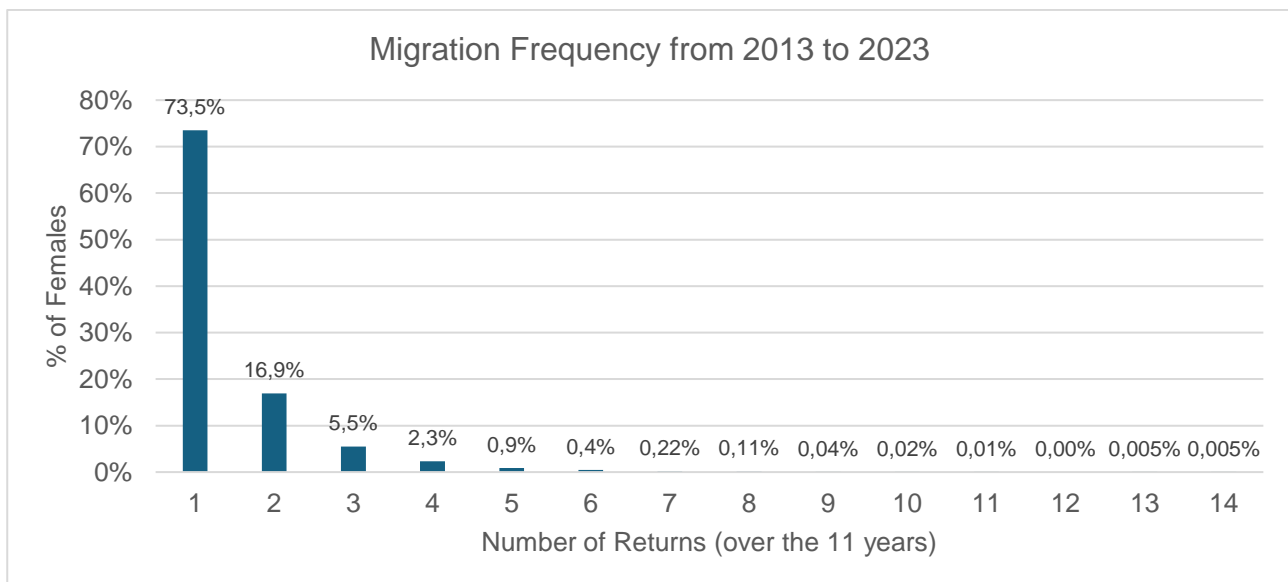


Figure 10: Number of returns per individual turtle over the 11 years

The database reported only three turtles returning 11 times over the 11-years period, and only two turtles returned 13 and 14 times (Tab. 5).

Table 5: Special cases of females that returned more than 10 times over the 2013-2023 period

Count of NEST PIT TAG	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	Grand Total
977200007415015	8					2		1				11
977200007755200	1		1		2		5		2			11
977200008668847		2			5					4		11
977200007390013	4		3		1		1	2		2		13
152109661A					5		7		2			14

Not surprisingly, there is a correspondence between some of the turtles that laid the highest number of nests and those that returned more frequently. The turtle identified by the PIT tag number "977200007390013" returned 13 times and laid 9 nests: only one out of four nesting events recorded

in 2013 and only two out of three events recorded in 2015 resulted in an oviposition. Similarly, the turtle tagged “152109661A”, the only turtle in the database that returned 14 times over the entire time period, laying nine nests in total.

A total of 2,118 tagged turtles have been emerging onto JB Beach without laying a nest. To investigate whether this Behavior was a sporadic event or whether the same individuals tended to repeat the pattern over the years and attempted nesting multiple times, a further analysis has been conducted. The results indicated that most of them, 93.53%, only attempted nesting once, while 117 and 16 turtles, respectively, attempted nesting two and three times (Fig. 11). Only four of them have been monitored while attempting nesting four times but never succeeded.

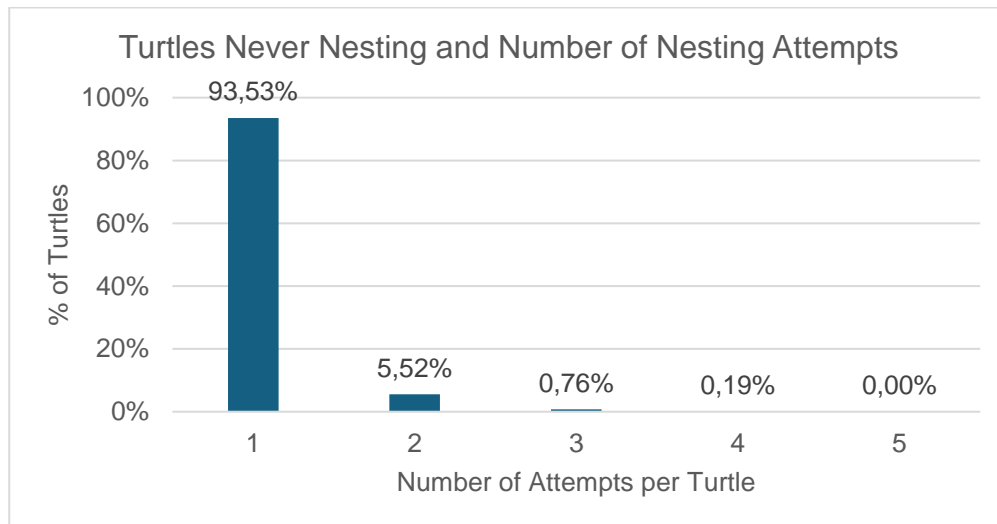


Figure 11: Number of turtles never nesting and their attempts

It is interesting to notice that the attempts have not been done all in the same nesting season, and that the same individuals migrated in different years (Tab. 6). This could exclude that the false crawl is due to disturbance or lack of an adequate location for a nest and might indicate a possible malformation or amputations that could impede essential stages in the oviposition such as digging. Considering the high uncertainty of the monitoring activity, these turtles might have nested without being monitored.

Table 6: Nesting attempts of turtles that have not been observed nesting

Count of NEST PIT TAG	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	Grand Total
941000026577021									4			4
977200008763648				2		2						4
977200009116387				2		2						4
132855217A						3				1		4

### 3.2. Number of Nests (NN) per Season

The Number of Nests (NN) laid by individual turtles within a nesting season revealed that the monitored females laid only 1.19 nests per year. However, as shown in Figure 12, of the 19,462 nesting females tagged in the population, 16,000 laid only 1 nest per year. Only 15.06% of the nesting females laid between one and two nests per season, while only 2.36% laid between two and three nests. From the available data, only 65 monitored turtles laid between three and four nests per season, while just six of them laid between four and five nests per season.



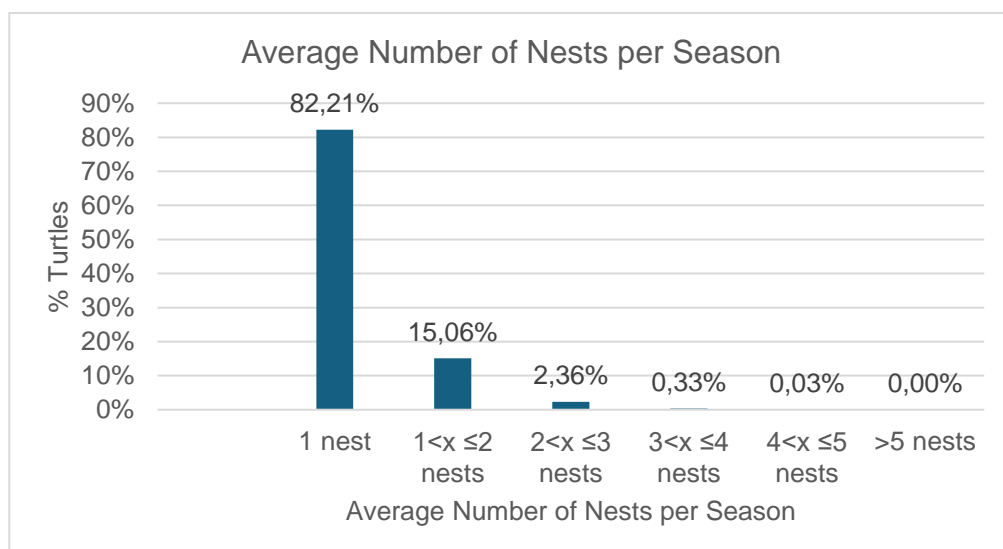


Figure 12: Average number of nests per season

It is important to stress that the averages are calculated only based on the data available in our database, which is far away from representing the real nesting activity happening in JB Beach. Although the database represents one of the largest available, if considering *Caretta caretta* sub-population nesting in the archipelago, the number of monitored turtles is still a small representation of the total number of females emerging onto JB Beach. In fact, we could affirm that Loggerhead females' nesting potential is much higher than the calculated value of 1.19 nests on average, which is low solely due to limitations in the monitoring program and not due to *Caretta caretta* reproductive Behavior and biology.

*Caretta caretta* females could potentially lay up to 5 or 6 nests in one season (Tab. 7), although the monitored cases evidencing this potential are relatively rare. Table 7<sup>5</sup> summarizes the number of cases recorded when individual turtles laid up to six nests in one season. The database reported 92 cases when individual turtles laid 4 nests within the same nesting season, and 11 cases when 5 nests have been laid within the same nesting season by individual turtles. Only one case has been observed when a turtle deposited six nests within one nesting season. Although these cases are the minority in our database, and do not contribute much to the arithmetic mean of Number of Nests per season, they are more reflecting reality.

Table 7: Number of nests per season - special cases

Number of nests per season	Number of cases recorded	% of cases
1	17835	83,14%
2	2923	13,63%
3	590	2,75%
4	92	0,43%
5	11	0,05%
6	1	0,005%
<b>TOT cases recorded</b>	<b>21452</b>	<b>100,00%</b>

<sup>5</sup> Important to notice is that the total of 21,452 reported in the table does not represent the total number of nesting females monitored (which is 19,462), but the total number of cases recorded (or nesting seasons). In fact, single turtles can have multiple nesting seasons, which are accounted individually in Table 7.



Based on the assumptions that Loggerhead females could potentially lay up to five or six nests per season, we could recalculate the average NN just considering these individuals. Table 8 reports the cases when five and six nests per season have been recorded, summarizing for each individual the number of nests laid in each nesting season they have been monitored. A total of 12 turtles have been included, the 11 individuals which nested 5 times in one season plus the one which laid 6 nests within the same nesting season. Calculating the average NN per season per each individual turtle (in the last column) and averaging these numbers, we obtain a second average NN of 4.11 nests per season, that might be more realistic than the first average NN of 1.19.

*Table 8: Number of nests per year - special cases of turtles with 5 and 6 nests per season*

Count of NEST												Average NN per season
PIT TAG	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	
977200008489451	5					1			1			2,33
137545151A	6							1				3,50
977200008325774		5										5,00
977200008672010			5									5,00
977200008331463		3			5							4,00
977200009095997					5			1				3,00
941000022737197							5					5,00
941000022741157						1			5			3,00
977200009203470					2				5			3,50
941000026591359										5		5,00
941000026591626										5		5,00
941000027088121										5		5,00
<b>Average NN</b>												<b>4,11</b>

A second analysis has been conducted to include all the recorded nesting activities, and not just those resulting in oviposition. In this second part, all false crawls and uncertain cases (176 observations marked as “Doubt” in the “Nest” column) have been incorporated to provide a broader perspective on the nesting potential of Loggerhead females, and to account as well for the 176 observations in doubt that could influence the average NN calculated above. By considering all the observed nesting attempts, the analysis could reflect a more realistic estimation of the reproductive effort, since the unsuccessful nesting attempts may be caused by human disturbances or environmental factors, such as unsuitable beach conditions or high predation risks. Understanding how often turtles attempted to nest could help to refine the assessment of their nesting frequency. This comprehensive approach also accounts for the possibility that some turtles may require multiple attempts before effectively laying a nest, a fact that would otherwise be ignored if considering only certain oviposition events.

The vast majority returned on average only once per season (Fig. 13). Of the 21,580 females tagged in total, 78.60% of them came only once per season, while only 3,596 of them registered between one and two returns per season. A small percentage, 3.64%, came between two and three times per season, while 0.82% of them returned between three and four times. Only five of them returned between six and seven times per season, while only one female returned between seven and eight times. None of them returned more than eight times per season.

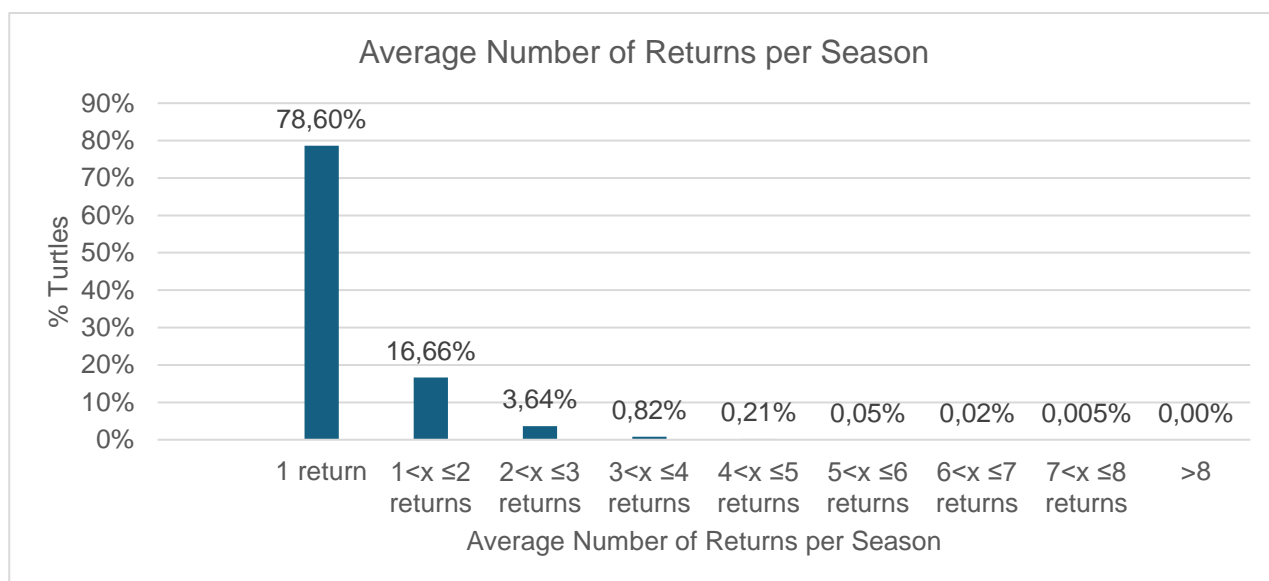


Figure 13: Average number of returns per season

Potentially, Loggerhead females could return up to seven or eight times per season in the attempt of laying a nest, as demonstrated by some cases recorded in the database. Table 9<sup>6</sup> summarizes the special cases in the dataset when individual turtles returned up to eight times in one season. Only 24 cases in the database had six returns within the same nesting season. Few turtles, specifically seven and two individuals returned seven and eight times, respectively, in one season.

Table 9: Number of returns per season - special cases

Number of returns per season	Number of cases recorded	% of cases
1	19253	79,60%
2	3617	14,95%
3	945	3,91%
4	264	1,09%
5	74	0,31%
6	24	0,10%
7	7	0,03%
8	2	0,01%
<b>TOT seasons</b>	<b>24186</b>	<b>100,00%</b>

These nine turtles are reported in Table 10, which summarizes, for each individual, the number of returns in the nesting seasons when they have been monitored. Calculating the average number of returns per season per each individual turtle (in the last column) and subsequently averaging them, we obtained a second average of 6.22 returns per season.

Although not many of the monitored turtles exhibited this potential and although these rare cases do not contribute much to increase the arithmetic mean of the number of returns per season, they can still be considered more representative of the reality. Once again, low numbers of returns per season

<sup>6</sup> Important to notice is that the total of 24,186 reported in Table 9 does not represent the total number of tagged females (which is 21,580), but the total number of cases recorded (or nesting seasons). Single turtles can return in multiple nesting seasons, and those are accounted separately in tTable 9, resulting in a total higher than 21,580.

can, indeed, reflect a limitation in the monitoring activities and not a constraint in the biology and reproductive potential of Loggerhead females.

Table 10: Number of returns per year - special cases of turtles with 7 and 8 returns per season

Count of NEST												Average returns per season
PIT TAG	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	
977200007415015	8					2		1				4
977200008325774		7				1						4
977200008329825		7										7
977200009094490					7							7
977200009208615					7							7
941000022737610						7						7
941000022743565							7					7
152109661A					5		7		2			5
981098108230181									8			8

### 3.3. Inter-Nesting Interval (INI)

The second nesting parameter is the Inter-Nesting Interval (INI), defined as the interval in days between two consecutive oviposition of the same individual. First, the average interval per each nesting female (PIT tag) was calculated. Subsequently, individuals have been clustered according to the length of their average interval. Consecutive nests with an interval bigger than 180 days – therefore, not within the same nesting season – have not been considered in this part of the analysis and later implemented for calculating the Remigration Interval (RI). To investigate the INI, only 22.9% of the 19,462 nesting females tagged in total were used, since 15,005 of them have been monitored only during one oviposition (Tab. 11). Within this 22.9%, only 17.79% of the turtles were used for the INI estimation, since they had at least two nests within the same nesting season, while 5.11% of them only laid nests with an interval longer than 180 days and therefore were only considered for the RI analysis.

Table 11: Average Inter-Nesting Interval per PIT tag

Average Inter-Nesting Interval per PIT Tag	Number of Turtles	% of Turtles
x=1 day	26	0,75%
1<x ≤7 days	30	0,87%
7<x ≤14 days	748	21,61%
14<x≤21 days	750	21,66%
21<x≤28 days	665	19,21%
x>28	1243	35,90%
<b>N turtles &lt;180 days</b>	<b>3462</b>	<b>17,79%</b>
<b>N turtles &gt;180 days</b>	<b>995</b>	<b>5,11%</b>
<b>N turtles 1 nest only</b>	<b>15005</b>	<b>77,10%</b>
<b>TOT Nesting Females</b>	<b>19462</b>	<b>100%</b>

Of the 3,462 nesting females included in the INI analysis, the vast majority laid with an interval greater than 28 days (Fig. 14). An almost equal share of them, 21.61% and 21.66% nested with an interval of 7 to 14 days and of 14 to 21 days, respectively. The analysis also revealed that some of the individuals, namely 0.87%, nested with an interval between one (excluded) and seven days, while 0.75% laid two nests with a one-day interval ( $x=1$ ). While the 26 turtles in the database nesting in the following day are, almost certainly, resulting from an error in data collection due to changes in patrolling shifts during the night and monitoring the same individual twice, the 30 individuals nesting within one week might give rise to some questions (Annex 2).

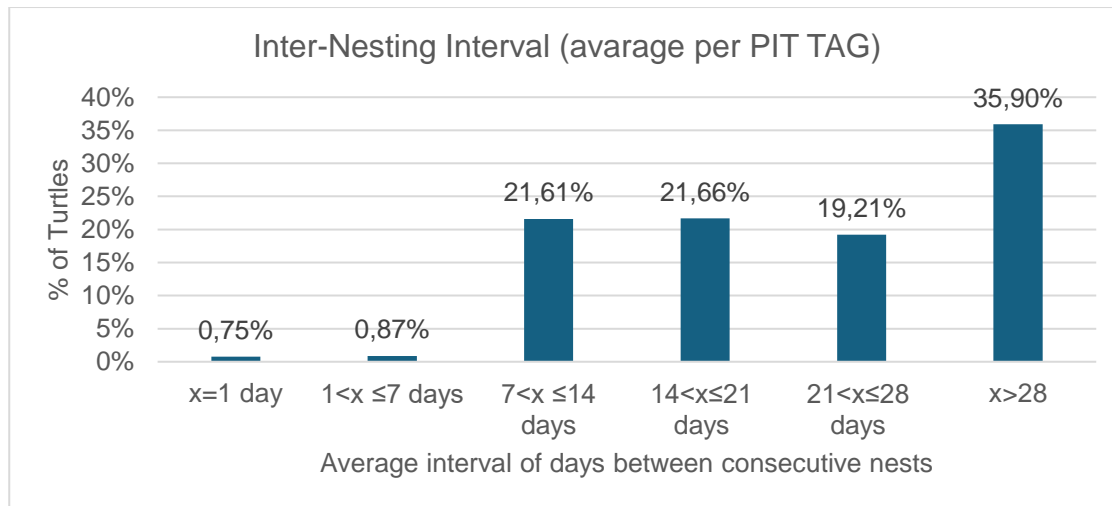


Figure 14: Inter-Nesting Interval (average per PIT tag)

After calculating the individual averages, an overall mean INI of 26.83 days has been calculated for the 3,462 nesting females included in the analysis (Table 14). Although being the best we can obtain, considering the limitations of the monitoring program, this estimation is still far from being a realistic representation of the nesting patterns of the Loggerhead sub-population nesting in Cape Verde.

In fact, if we consider the special cases of the 12 turtles nesting more frequently as reported in Table 8, a more realistic estimation of the Inter-Nesting Interval may be calculated. Table 12 summarizes the nesting dates<sup>7</sup> for these 12 individuals and reports the interval between consecutive nests within the same season. This analysis allows to assess the nesting potential of the sub-population and enables to conclude that females can nest up to five or six times within a nesting season, with an average INI of 15.85 days in between two consecutive oviposition. One observation needs to be done regarding PIT tag 941000026591626, since, as reported in Table 12, this individual is an example of a probable error in data collection: according to the available data, this female laid two nests within two days, on the 11<sup>th</sup> and on the 12<sup>th</sup> of July 2022. If we exclude the one on the 12<sup>th</sup>, considering it just as a repetition due to the change in patrolling team, the average INI for this individual could be recalculated as 14.33 days, changing the overall average INI for these 12 individuals to 16.15 days. This revised value of 16.15 days provides a more representative estimate of the average INI for the entire sub-population (Table 14).

<sup>7</sup> In Table 12, single nests laid within other nesting season have not been considered, since not relevant for the INI analysis. For instance, for the PIT tag 977200008489451, the single nest recorded in 2018 and 2021 have not been included.

Table 12: INI of turtles nesting more frequently

PIT TAG	DATE of NESTS	INTERVAL BETWEEN NESTS (DAYS)	INTERVAL CATEGORY	Avarage INI per PIT TAG
977200008489451	18/07/2013	16	14 < x ≤ 21 Days	15,25
977200008489451	03/08/2013	16	14 < x ≤ 21 Days	
977200008489451	19/08/2013	14	7 < x ≤ 14 Days	
977200008489451	02/09/2013	15	14 < x ≤ 21 Days	
977200008489451	17/09/2013			
137545151A	06/07/2013	18	14 < x ≤ 21 Days	16
137545151A	24/07/2013	18	14 < x ≤ 21 Days	
137545151A	11/08/2013	15	14 < x ≤ 21 Days	
137545151A	26/08/2013	16	14 < x ≤ 21 Days	
137545151A	11/09/2013	13	7 < x ≤ 14 Days	
137545151A	24/09/2013			
977200008325774	19/07/2014	17	14 < x ≤ 21 Days	14,50
977200008325774	05/08/2014	14	7 < x ≤ 14 Days	
977200008325774	19/08/2014	14	7 < x ≤ 14 Days	
977200008325774	02/09/2014	13	7 < x ≤ 14 Days	
977200008325774	15/09/2014			
977200008672010	20/07/2015	2	1 < x ≤ 7 Days	16,5
977200008672010	22/07/2015	14	7 < x ≤ 14 Days	
977200008672010	05/08/2015	24	21 < x ≤ 28 Days	
977200008672010	29/08/2015	26	21 < x ≤ 28 Days	
977200008672010	24/09/2015			
977200008331463	14/07/2014	31	28 < x ≤ 180 Days	19,17
977200008331463	14/08/2014	14	7 < x ≤ 14 Days	
977200008331463	28/08/2014			
977200008331463	05/07/2017	16	14 < x ≤ 21 Days	
977200008331463	21/07/2017	14	7 < x ≤ 14 Days	
977200008331463	04/08/2017	15	14 < x ≤ 21 Days	
977200008331463	19/08/2017	25	21 < x ≤ 28 Days	
977200008331463	13/09/2017			
977200009095997	12/07/2017	16	14 < x ≤ 21 Days	16,25
977200009095997	28/07/2017	25	21 < x ≤ 28 Days	
977200009095997	22/08/2017	12	7 < x ≤ 14 Days	
977200009095997	03/09/2017	12	7 < x ≤ 14 Days	
977200009095997	15/09/2017			
941000022737197	13/07/2019	17	14 < x ≤ 21 Days	15,5
941000022737197	30/07/2019	15	14 < x ≤ 21 Days	
941000022737197	14/08/2019	16	14 < x ≤ 21 Days	
941000022737197	30/08/2019	14	7 < x ≤ 14 Days	
941000022737197	13/09/2019			
941000022741157	30/06/2021	17	14 < x ≤ 21 Days	18

941000022741157	17/07/2021	17	14 < x ≤ 21 Days	
941000022741157	03/08/2021	25	21 < x ≤ 28 Days	
941000022741157	28/08/2021	13	7 < x ≤ 14 Days	
941000022741157	10/09/2021			
977200009203470	25/08/2017	27	21 < x ≤ 28 Days	
977200009203470	21/09/2017			
977200009203470	06/08/2021	4	1 < x ≤ 7 Days	
977200009203470	10/08/2021	26	21 < x ≤ 28 Days	17
977200009203470	05/09/2021	15	14 < x ≤ 21 Days	
977200009203470	20/09/2021	13	7 < x ≤ 14 Days	
977200009203470	03/10/2021			
941000026591359	06/07/2022	16	14 < x ≤ 21 Days	
941000026591359	22/07/2022	13	7 < x ≤ 14 Days	
941000026591359	04/08/2022	25	21 < x ≤ 28 Days	16,75
941000026591359	29/08/2022	13	7 < x ≤ 14 Days	
941000026591359	11/09/2022			
941000026591626	11/07/2022	1	x=1	
941000026591626	12/07/2022	15	14 < x ≤ 21 Days	
941000026591626	27/07/2022	13	7 < x ≤ 14 Days	10,75
941000026591626	09/08/2022	14	7 < x ≤ 14 Days	
941000026591626	23/08/2022			
941000027088121	29/07/2022	7	1 < x ≤ 7 Days	
941000027088121	05/08/2022	6	1 < x ≤ 7 Days	
941000027088121	11/08/2022	16	14 < x ≤ 21 Days	14,5
941000027088121	27/08/2022	29	28 < x ≤ 180 Days	
941000027088121	25/09/2022			
<b>Average INI</b>				<b>15,85</b>

As previously done in Paragraph 3.2., also for this parameter a second analysis was performed to include all recorded nesting activities - not only those resulting in oviposition. In this extended analysis, false crawls and uncertain cases were also considered to provide a broader perspective on the nesting potential of Loggerhead females and to address the additional factors discussed earlier. This variation of the INI parameter obtained in this way will be addressed as Inter-Migration Interval (IMI) since it is considering all the emergencies and it describes the average interval between two consecutive returns. This provides information of the migration frequency within a nesting season.

Following the same path as above also for the IMI analysis, the average interval per each PIT tag was calculated. Individuals have been clustered according to the length of their average interval. Consecutive returns with an interval longer than 180 days have not been considered here but have been later included for the RI calculation. To investigate the IMI, only 20.83% of the 21,580 females tagged have been used, since 73.51% of them have been monitored only once, while another 5.17% only returned in different nesting seasons (Table 13). The remaining 0.49% are the turtles with duplicate nesting events, that have not been considered in the analysis.

Unlike as in Table 11, where each individual was classified into a single Inter-Nesting Interval (INI) category, ensuring that the total number of nesting females (19,462) was obtained without

discrepancies, Table 13 accounts for all tagged females (21,580) required to additionally account for the duplicate values (105). This discrepancy arises because of the 277 duplicate values in the dataset (273 PIT tags, of which 4 were duplicated twice) that have been excluded from the analysis. However, only 105 cases (where the interval category would be  $x=0$ ) were missing from the category sum, as the other PIT tags have been accounted for within the other interval categories because of the other nesting events attributable to them. Since these duplicates inflated the overall dataset (with 277 extra duplicate observations that have been excluded for the analysis) but not the count of unique individuals, they needed to be explicitly accounted for to maintain consistency in the total of tagged females. Only 105 of these 273 PIT tags with duplicate values had two nests in the same day (cases with “Yes” & “Yes” in the “Nest” column), while the other PIT tags have been recorded in the database during other nesting events, which allowed to them to be included in the other interval categories.

Table 13: Average Interval Between Consecutive Returns per PIT Tag

Avarage Inter-Migration Interval per PIT TAG	Number of Turtles	% of Turtles
$x=1$ day	125	2,78%
$1 < x \leq 7$ days	144	3,20%
$7 < x \leq 14$ days	1016	22,60%
$14 < x \leq 21$ days	1048	23,31%
$21 < x \leq 28$ days	778	17,30%
$x > 28$	1385	30,81%
<b>N turtles &lt;180 days</b>	<b>4496</b>	<b>20,83%</b>
<b>N turtles &gt; 180 days</b>	<b>1116</b>	<b>5,17%</b>
<b>1 return only</b>	<b>15863</b>	<b>73,51%</b>
<b>N turtle with duplicate values (<math>x=0</math>)</b>	<b>105</b>	<b>0,49%</b>
<b>TOT tagged females</b>	<b>21580</b>	<b>100%</b>

Of the 4,496 females included in the IMI analysis, the vast majority laid with an interval greater than 28 days (Fig. 15).

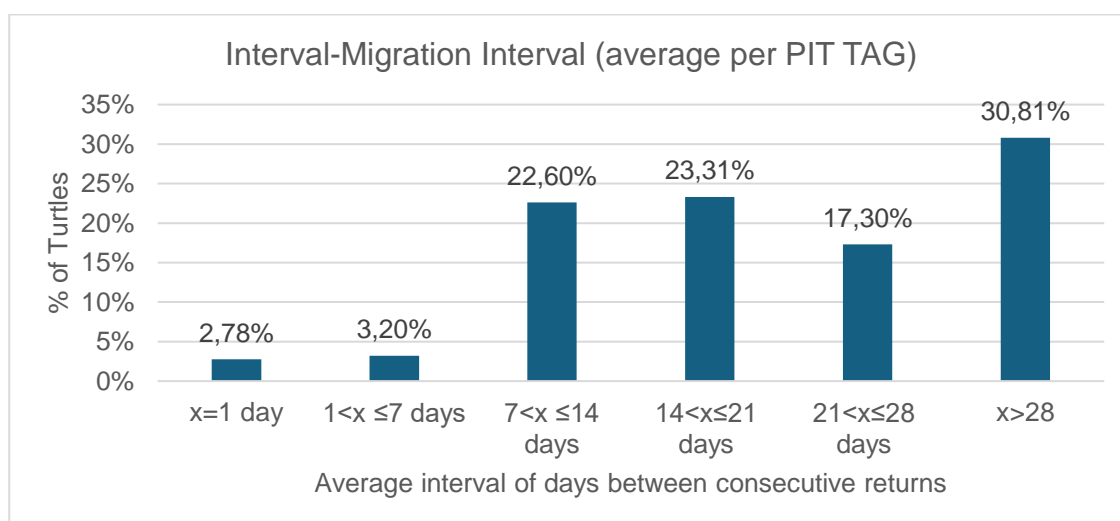


Figure 15: Interval Between Consecutive Returns (average per PIT Tag)



An almost equal share of them, 22.6% and 23.31%, nested with an interval of 7 to 14 days and of 14 to 21 days, respectively, reflecting the trend seen also in the INI. A total of 3.20% returned with an average interval between 1 and 7 days, while 2.78% of them returned the following day ( $x=1$ ), probably emerging for the same nest if the first-time oviposition was not possible.

After calculating the individual averages, an overall mean IMI of 24.28 days has been calculated for the 4,496 females included in the analysis (Table 14), a value that could best describe the migration trend of this sub-population.

However, if we consider - as we previously did with the INI - the special cases of the nine turtles monitored more frequently reported in Table 9, a more realistic estimation of the IMI may be calculated. Following the same path as before, the nesting dates for these nine individuals have been summarized in Annex 3<sup>8</sup>. An average IMI between consecutive returns within the same season has been calculated for each individual turtle. This analysis allowed the assessment of the migration potential of the sub-population resulting in seven or eight returns of females within a nesting season with an average IMI of 10.87 days in between two consecutive returns (Table 14).

*Table 14: Average Inter-Nesting Interval and average Inter-Migration Interval in the population*

Parameters	Days
Inter-Nesting Interval (population average)	26,83
Inter-Nesting Interval revisited (with only more frequently nesting turtles)	16,15
Inter-Migration Interval (population average)	24,28
Inter-Migration Interval revisited (only with turtles migrating more frequently)	10,87

### 3.4. Remigration Interval (RI)

The third nesting parameter analyzed in this research is the Remigration Interval (RI), defined as the number of years between successive nesting seasons for individual turtles. It describes the interval in years in-between one nesting season and the following, offering an insight into the duration of a female's ovulation cycle and the process of energy accumulation for reproduction. The RI analysis revealed significant variation among nesting females.

To analyze this parameter, only a small percentage of the females in the dataset was used. Of the 19,462 total nesting females, only about 10% (1,780 turtles) have been monitored nesting at JB Beach for more than one season. Figure 16 illustrates the total number of nesting seasons per turtle across the 11-years period. A total of 90.85% of the individuals were recorded nesting in only one season, while a progressively smaller number of turtles were monitored for two or more nesting seasons. Only 187 turtles were recorded nesting in three seasons, while only five of them have been seen nesting for four seasons. This result can be, again, either a demonstration of the limitations in the monitoring program - since turtles might have returned to nest more often but might not have been recorded - or an indication of a not absolute site-fidelity among some individuals. It might suggest that while some turtles exhibit site-fidelity over multiple years, a large proportion of individuals do not return to nest within the observed timeframe. It could also be proof of a very high mortality especially among adults and especially in foraging areas such as Mauritania, probably due to fishing activities and extreme poverty of fishermen, a fact that has only been suspected until now.

<sup>8</sup> In Annex 3, for the two PIT tags 977200008329825 and 981098108230181 only one of the two emergencies recorded in the same night have been considered for the IMI analysis. None of the emergencies on 14/08/2014 for the PIT tag 977200008329825 resulted in a nest, while for the PIT tag 981098108230181 only one of the two emergencies resulted in an oviposition.



However, three females in the database returned to nest for five seasons, while there is also evidence of one case when a turtle nested over six seasons in 11 years. Although only being a single observation, this rare case indicates the nesting potential of Loggerhead turtles which, according to literature, rarely ovulate for two consecutive years.

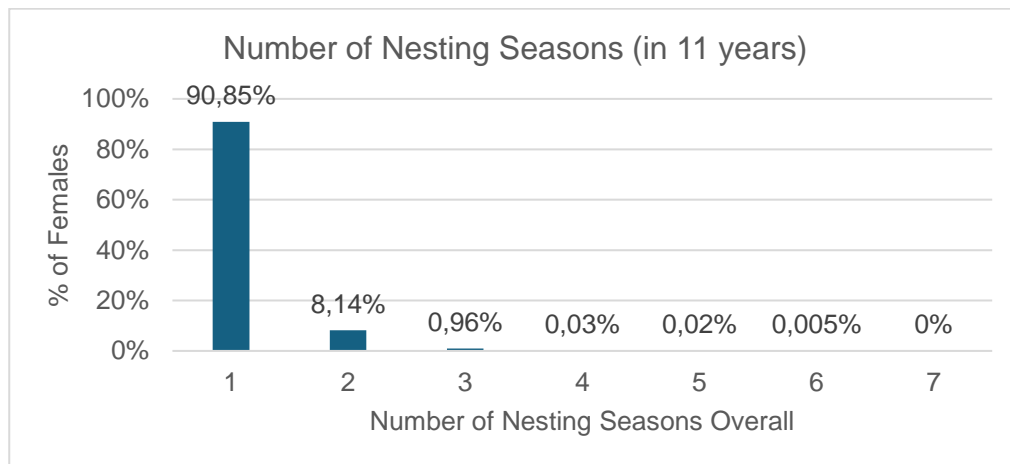


Figure 16: Number of nesting seasons per turtle in the 11-years period

Among the 1,780 turtles recorded at least in two different seasons, the distribution of RIs has been investigated and summarized in Table 15. It is important to note that, unlike in the previous analysis where averages per individual turtles were calculated, in this case, each individual RI was accounted for separately. This means that if a turtle exhibited different remigration intervals across different nesting seasons it was counted more than once, resulting in an exceeding total count of RIs (1,911) in respect to the total number of nesting females analyzed (1,780). This approach allowed for a more comprehensive overview of the variability in RIs within the sub-population, describing all the observed patterns and highlighting special cases observed rather than just individual averages.

Table 15: Remigration Interval

Interval Years	Number of Turtles	N Turtles nesting with the same pattern:				% of Turtles
		x1 time	x2 times	x3 times	x4 times	
1	55	51	4			3,09%
2	531	489	37	2	3	29,83%
3	831	810	21			46,69%
4	265	261	4			14,89%
5	139	139				7,81%
6	42	42				2,36%
7	29	29				1,63%
8	15	15				0,84%
9	3	3				0,17%
10	1	1				0,06%
TOT	1911					100,00%
TOT females	1780					
RI (weighted average)	3.13					

An average RI representing a generalized nesting pattern of the sub-population was determined by calculating a weighted mean among all observed year intervals and the number of turtles that nested with that RI. The resulted average RI of 3.13 years (Table 15) indicates that, in line with the literature,

turtles generally returned to nest approximately every three years. However, in specific cases, some individuals returned after shorter intervals, such as two or even just one year.

The most common RI was 3 years, with 46.69% of the 1,780 turtles nesting with this interval at least once, followed by 2 years (29.83%) and then four 4 years (14.89%). Longer intervals beyond five years were progressively rarer, potentially indicating a lack in data collection. In Figure 17 these cases are indicated in orange, to distinguish them from the more reliable and realistic data.

Of the 531 turtles that nested with a two-year interval, 489 only did it once, 37 of them nested with this interval twice, while 2 and 3 turtles nested following this pattern 3 and 4 times, respectively, an impressive fact considering the energy that the whole reproductive cycle requires. It is also interesting to note that 55 turtles nested with a RI of one year. Of these 55 turtles, 51 of them nested with this pattern only once, while 4 of them followed this pattern twice in the 11-years period.

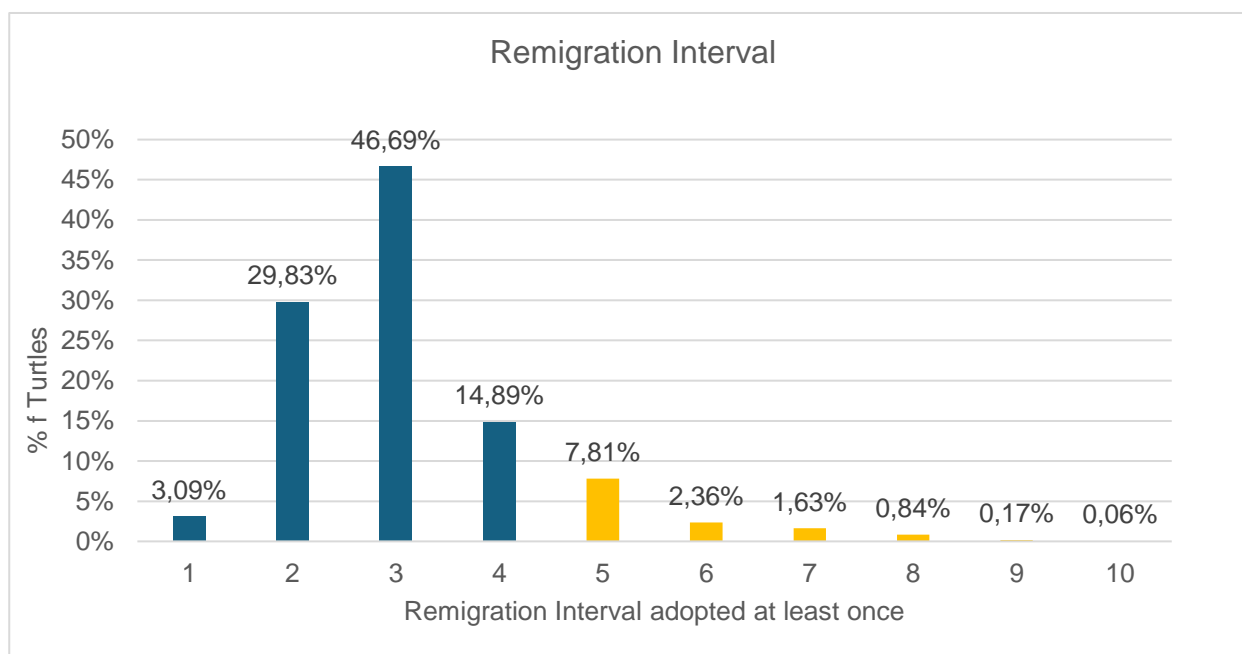


Figure 17: Remigration Interval

Table 16 reports the special cases highlighted in Table 15, where turtles exhibited the same nesting pattern across multiple seasons. This allows for an assessment of whether these intervals were sporadic occurrences or whether certain individuals consistently returned to nest following the same pattern. Some individuals (highlighted in green) consistently returned at shorter intervals, e.g. every one or two years. The two PIT tags 977200008328919 and 977200008663132, for instance, had a 1-year interval between the first and the second nesting season (NS), then waited two years in-between the second and the third NS, and then nested again in the fourth nesting season with a 1-year interval from the previous one. The two PIT tags highlighted in pink nested with a 2-year interval four times, while PIT tag 977200007390013 even nested with a 1-year interval in-between the fourth and the fifth nesting season.

These cases demonstrate that, although the population exhibited a generalized trend of nesting every three years on average, remigrations intervals can be an individual-specific trait rather than a uniform pattern across the population, and that individual turtles tend to follow their own remigration cycles. The recurrence of specific intervals within individuals suggests that remigration behavior

tends to vary from one individual to another, and that it may be influenced by environmental and physiological factors such as food availability and fitness levels.

Table 16: Turtles exhibiting the same remigration pattern across multiple nesting seasons (NS)

PIT TAG	Year interval between:					Average Year Interval
	1-2 NS	2-3 NS	3-4 NS	4-5 NS	5-6 NS	
941000020404886	1	1				1,00
977200008328919	1	2	1			1,33
977200008663132	1	2	1			1,33
977200009094394	2	1	1			1,33
<b>977200007752454</b>	2	2	2	3		2,25
977200008496280	2	2	2			2,00
<b>977200007390013</b>	2	2	2	1	2	1,80
<b>977200007755200</b>	2	2	2	2		2,00
<b>977200008662540</b>	2	2	2	2		2,00
977200008333004	4	4				4,00
977200008494632	4	4				4,00
130911730A	4	4				4,00
133331793A	4	4				4,00

Finally, an average Remigration Interval per PIT tag has also been calculated and summarized in Figure 18, reinforcing the prevalence of remigration cycles between two and three years. Of the 1,780 turtles included in the RI analysis, 45.06% presented this average RI ( $2 < x \leq 3$ ). A total of 26.07% nested with an average interval between one and two years, while 2.13% with an average of 1-year interval. Average intervals greater than five years (in orange) might be a demonstration of the limitations in the monitoring program. Calculating an average RI for the sub-population with the average RI of individual turtles, the resulting 3.14 years interval is reflecting the previously calculated weighted average of 3.13 years. This result aligns with findings from other studies on *Caretta caretta*, suggesting that while variability exists, a three-year cycle remains the most common pattern.

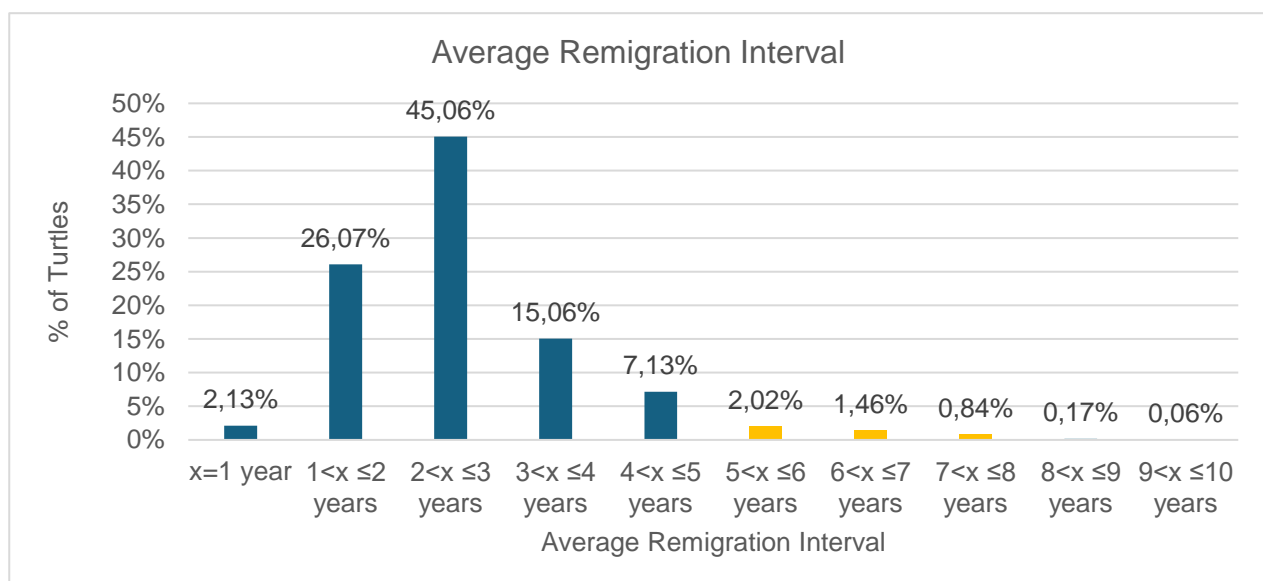


Figure 18: Average Remigration Interval

Also for this parameter, a second analysis was performed including all recorded nesting activities and not solely those resulting in oviposition to provide a more comprehensive perspective on the remigration patterns of Loggerhead turtles. In this analysis, all the emergencies and nesting attempts, not only the successful ones, have been considered.

Figure 19 illustrates the number of seasons in which individual turtles have been seen returning to JB over the 11-year period. Compared to the previous analysis, which focused exclusively on confirmed nests, a higher number of individuals were recorded returning across multiple seasons, since some females attempted nesting in multiple years but did not always complete the oviposition process. The majority was observed at JB only in one nesting season. Of the 21,580 females tagged in total, 10.61% were monitored in at least another nesting season. These 2,290 individuals were used for the extended RI analysis. Only 17 of them were recorded in four nesting seasons, while 3 of them in 5 seasons. Only one turtle has been recorded for six nesting seasons within the 11-years period. This turtle together with the three turtles that returned five times are the same four turtles that nested most frequently (Fig. 16). For this reason, these 4 PIT tags are reported in bold in Table 16 and Table 18, and in Table 19.

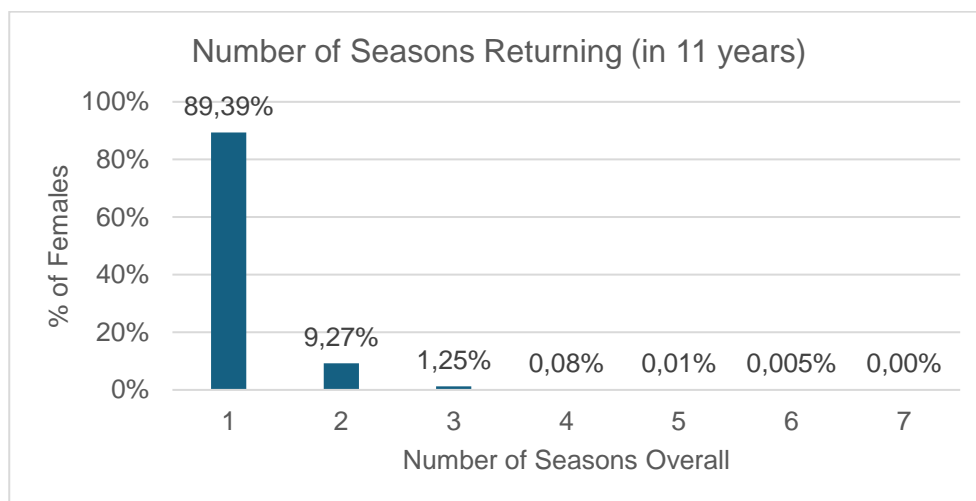


Figure 19: Number of seasons in which individual turtles were seen returning over the 11 years

Table 17 summarizes the distribution of RIs when considering all returns. It needs to be noticed that in this table as previously in Table 15, the single intervals are considered – so that if turtles returned at least once with that interval - and not the average of intervals per individual turtles. For this reason, turtles returning in multiple nesting seasons with different RIs are accounted more than once, resulting in a total (2,487) higher than the total number of turtles included in this extended analysis (2,290).

Figure 20 visualizes the distribution of RIs in this expanded dataset and shows that the general trend remains consistent with previous findings. The majority of individuals showed a three-year remigration cycle, but a notable fraction exhibited a two-year or even a one-year interval. Of the 2,290 individuals, 46.86% returned after three years, 29.61% after two years, and 16.59% after four years. A small percentage, 3.06%, returned with a 1-year interval: 64 of these returned with this interval only once, while the other 6 turtles followed this pattern twice. These six turtles, together with the seven and three turtles that returned at a 2-year interval three and four times, respectively, are reported in Table 18.

The weighted average RI in this extended analysis is 3.39 years, slightly higher than the 3.13 years previously calculated when only successful nesting events were considered.

Table 17: Remigration Interval considering all the nesting events

Interval Years	Number of Turtles	N Turtles returning with the same pattern:				% of Turtles
		x1	x2	x3	x4	
1	70	64	6			3,06%
2	678	618	50	7	3	29,61%
3	1073	1039	34			46,86%
4	380	374	6			16,59%
5	187	187				8,17%
6	51	51				2,23%
7	28	28				1,22%
8	17	17				0,74%
9	2	2				0,09%
10	1	1				0,04%
TOT	2487					100,00%
TOT females	2290					
RI (weighted average)	3.39					

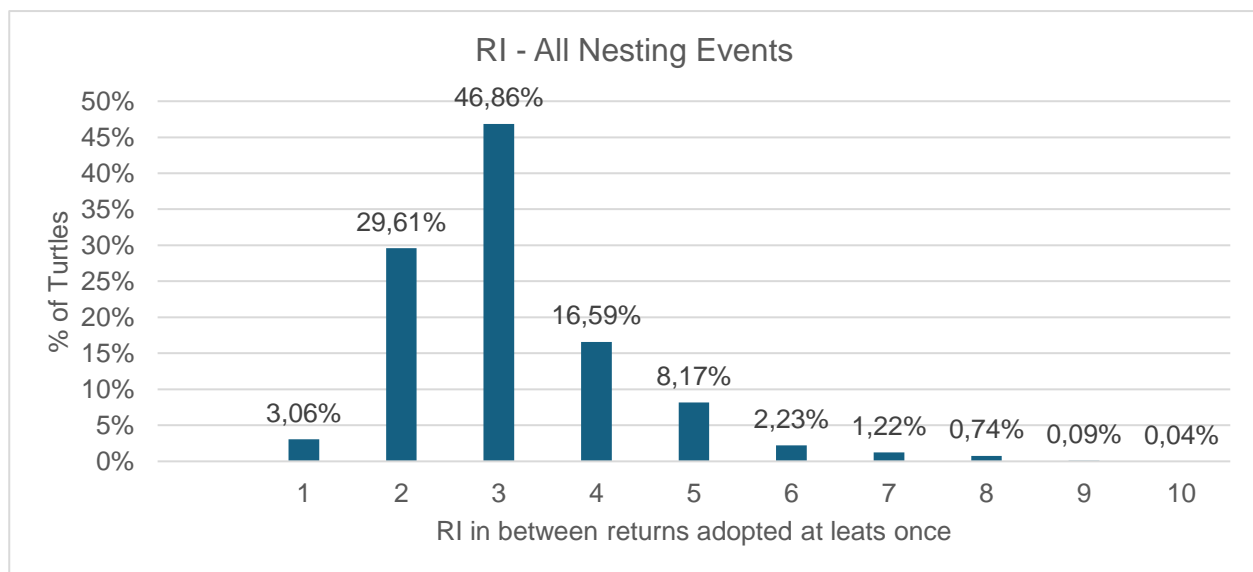


Figure 20: RI considering all the nesting events

Table 18 further explored the cases highlighted in Table 17, when turtles exhibited consistent RI patterns across multiple seasons. This allowed to assess whether short remigration intervals were sporadic occurrences or represented a repeated Behavioral pattern. The results reinforced the assumption that remigration cycles are individual-specific, rather than a uniform pattern across the population. Furthermore, certain turtles can consistently return at shorter intervals, while others can maintain longer gaps between nesting seasons, a behavioral trait that might potentially reflect differences in the fitness level, food availability or other environmental and physiological factors.

The four PIT tags reported in bold in Table 18 are the turtles that returned (and nested) more frequently in the whole database, with an RI between 1.8 and 2.25 years (Tab. 19).

Table 18: Special cases of turtles exhibiting the same RI across multiple seasons (R=Returns)

PIT TAG	Year interval between:					Average Year Interval
	1-2 R	2-3 R	3-4 R	4-5 R	5-6 R	
941000020404886	1	1				1,00
977200007734439	1	1				1,00
977200008328919	1	2	1			1,33
977200008660330	2	1	1			1,33
977200008663132	1	2	1			1,33
977200009094394	2	1	1			1,33
977200007735267	2	2	2			2,00
<b>977200007752454</b>	2	2	2	3		2,25
977200008496280	2	2	2			2,00
977200008662199	2	2	2			2,00
977200008664967	2	2	2			2,00
977200008670722	2	2	2			2,00
977200009155192	2	2	2			2,00
<b>977200007390013</b>	2	2	2	1	2	1,80
<b>977200007755200</b>	2	2	2	2		2,00
<b>977200008662540</b>	2	2	2	2		2,00

Table 19 reports, for each PIT tag, both the oviposition only (in the grey rows) and the nesting events overall (white rows), independent of being successful or not.

Table 19: The 4 turtles returning (white rows) and nesting (grey rows) during 5 and 6 nesting seasons

PIT TAG	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	N of nesting seasons	Average Year Interval
977200007390013	1		2		1		1	2		2		6	1,80
977200007390013	4		3		1		1	2		2		6	1,80
977200007752454		1		2		1		1			1	5	2,25
977200007752454		2		4		1		1			1	5	2,25
977200007755200	1		1		1		3		1			5	2,00
977200007755200	1		1		2		5		2			5	2,00
977200008662540		1		1		1		1		1		5	2,00
977200008662540		1		1		4		1		1		5	2,00

Finally, also in this extended analysis, an average RI per PIT tag has been calculated and summarized in Figure 21, reflecting the same pattern observed previously and reinforcing the prevalence of remigration cycles between 2 and 3 years. Of the 2,290 turtles 24.98% returned within one and two years, while 2.18% returned with an average interval of one year. The average RI calculated based on these individual averages is 3.13 years, similar to the one calculated above.

Overall, this result confirms again that, even if a three-year cycle remains the most common pattern, variability still exists among individuals and that RI may be influenced by various environmental and physiological factors, such as sea temperature that affects food availability, nesting site fidelity, reproductive readiness, and foraging area, if females feed in different habitats. The inclusion of all

nesting attempts provides a broader understanding of how frequently females return to nest providing an insight into the complexity of remigration dynamics in this sub-population.

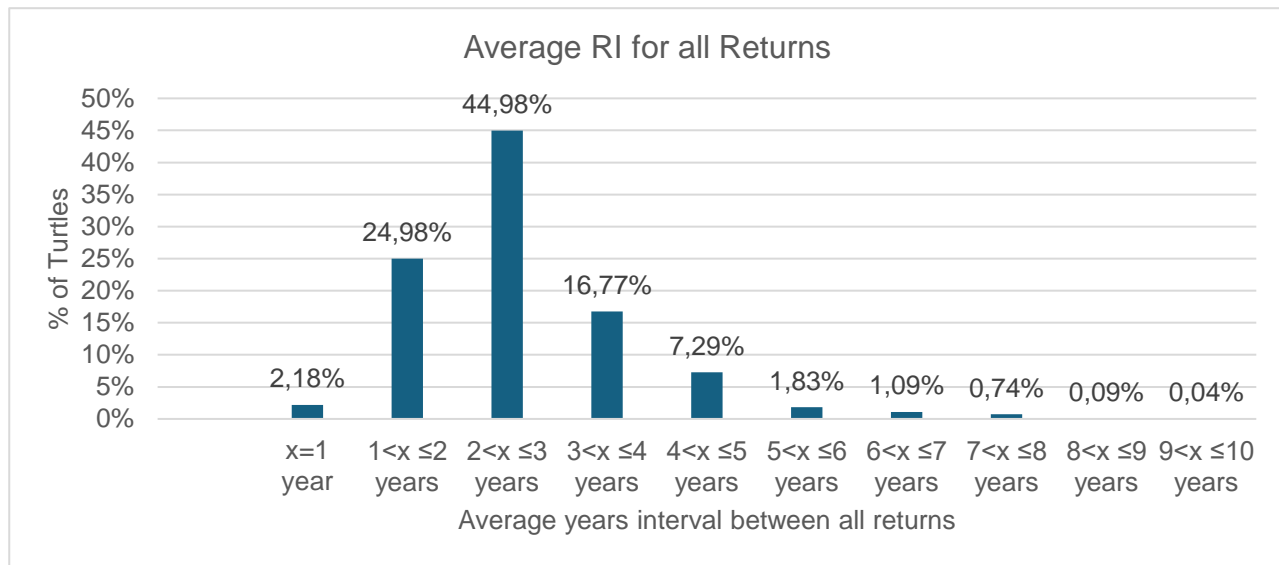


Figure 21: Average Remigration Interval considering all the nesting events

## 4. Discussion

### 4.1. Interpretation of Results

The results presented in this study offer an estimation of the three nesting parameters under analysis and help to understand the nesting Behavior of the Northeast Atlantic Loggerhead sub-population nesting in Cape Verde. However, it is important to acknowledge that the observed values are affected by multiple factors, such as migration patterns, mortality rates and limitations in the monitoring program. Therefore, the data analyzed here are our best values and represent the best available estimates but are by no means absolute values and are conservative estimates.

#### 4.1.1. Population Trends and Overview

From the available data, a generally increasing trend in the nesting population is apparent (Fig. 6). This suggests a recovery over the last years; however, a cautious interpretation is necessary to avoid a premature and excessively optimistic conclusion. Several hypotheses connected to anthropogenic pressure and climate change could explain this increase. One possible explanation could be the significant decrease in the numbers of the main predator of sea turtles, sharks, which are indeed facing a severe decline in some regions of Cape Verde over the last decades. Although not many specific estimates are yet available, some published articles and the direct experience of local fishermen and oral testimonies point towards a declining shark population in this region of the Atlantic. A recent study reports that 66% of the 53 shark species found in Cape Verde are threatened by extinction due to fishing and habitat degradation (Varela et al., 2025). This substantial decline in shark populations could significantly affect the number of sea turtles approaching the sandy beaches of Boa Vista to nest by potentially decreasing predation pressure on them.

Another factor determining an increase in the number of females coming to nest in João Barrosa and, therefore, an increase in the number of nests, could be a change in the availability of other nesting sites. Increased tourism and construction work in other beaches of Boa Vista or around other Cape Verdean islands could impact sea turtles' nest fidelity and push them to search for other more

isolated and undisturbed beaches. João Barrosa's location makes it an ideal place to nest due to its geographic position in the south-east part of the island. Here, a paved road has not yet been constructed, and tourist infrastructures and light pollution are minimal. This makes JB Beach a completely isolated location with very low anthropogenic impact, beside controlled ecotourism activities such as turtle-watching tours and the monitoring activities. Furthermore, its 5 km-long sandy coastline provides ideal conditions for nesting, and the absence of major land-based predators such as felines and canines reduce nest predation risks which come mainly from crows and ghost crabs (*Ocypode cursor*). Therefore, turtles previously nesting on other beaches or juveniles that otherwise would choose their birthplace to nest could shift and land at this beach, resulting in the observed increase in population size. It would be interesting to evaluate the impact that the construction of the large-scale coastal resort "Hotel Riu Touareg" has on nesting activities in JB since its opening in May 2011 on Lacacão Beach at the southern part of Boa Vista Island approximately 10 km away from JB. Already at its initial construction phase, Riu Touareg resort severely impacted nesting activities at Lacacão Beach (Turtle Foundation, 2011), suggesting that some displacements of nesting activity to JB might have occurred.

Furthermore, conservation programs implemented over the last decades at JB and adjacent beaches may now be yielding results and represent another reason for the increase in nesting activity recorded. Given that *C. Caretta* can attain maturity at 10-39 years (Avens and Snover 2013), depending on the environmental conditions, it is plausible that the rise in nesting numbers reflects the results of past conservation efforts with hatchlings emerged 15/20 years ago returning to their natal beaches to nest. Lastly, another consideration to be made is that such an increase in nesting population, although showing a linear trend in the last 11 years, could be a cyclical or temporary trend and could decrease again in the near future.

For all the reasons mentioned above and considering the endangered status of this sub-population, it would be too early to infer an increase in population size by only looking at the number of individuals nesting in JB over the last years. Also, a comparison with the number of individuals and nests on other beaches of Boa Vista and on other Cape Verdean islands should be implemented to verify whether the increase seen in João Barrosa can be linked to a decrease or an increase in the number of individuals nesting elsewhere. However, it can be reasonably concluded that the observed increase in nesting activities is not due to varying sampling efforts as the monitoring program tried to ensure consistency in the number of monitors over the years to avoid biases. Only in the high-activity years, the association introduced some variations in order to be able to face the increase in nesting females.

Besides the notable increase in nesting females over the last years, another interesting result emerged from the data analysis was the number of new turtles tagged every year (Fig. 8). The percentage of recaptured and newly tagged individuals is an important metric for assessing population stability. A constant ratio across the years of newly tagged versus recaptured females suggests a relatively stable reproductive group, not excessively influenced by external factors causing drastic shifts in the nesting population. However, the fact that new individuals continue to be tagged at a high rate over a decade may suggest high shifts in nesting population and elevated mortality rates among adults. In a population with low mortality of adults, the trend would be different than the one shown in Figure 8. The mortality rates in Cape Verde, although still present in the open ocean due to uncontrolled fishing activities (intentional or as a bycatch), it drastically decreased over the last decades as a result of the conservation programs and monitoring activities implemented across most of the sandy beaches in the archipelago. Also increased tourism might have indirectly played a partially positive role in mitigating mortality, since locals that earlier were responsible of



turtles and eggs poaching are now employed in the tourism sector, one of the main sectors of economic development in Cape Verde, responsible of the 20.1% of the national gross domestic product and generating more than 36,000 jobs (Marco et al., 2021). Therefore, considering the decreased mortality in the nesting grounds, a high mortality can be assumed offshore particularly in the foraging areas, along the West African coast.

Interestingly, in 2020 and 2021, during the pandemic years, nesting activity increased noticeably, reaching a peak in 2021 (Fig. 6 & Fig. 7), and these two years were also the ones with the highest percentages of newly tagged individuals. Both in 2020 and 2021, the recaptured females represented only about the 21% of the total females monitored at JB in these two years - the lowest percentages in the 11-year period of analysis (Fig. 8). This fact raises new questions about the possible factors causing it. A possible explanation could be that more females reached reproductive maturity in those years, perhaps due to a synchronization happened in the sea among juveniles. This phenomenon could be possibly explained by an increase in food availability or other environmental factors, such as sea temperature and salinity, that accelerated maturity and influenced their reproductive output. Further studies would be needed to address these hypotheses and investigate potential correlation between these factors and an acceleration in reproductive maturity.

It cannot be excluded, that the Covid pandemic had a positive impact on, at least, the population mortality and food availability, possibly influencing the peaks recorded in 2020 and 2021 in the nesting activity. We can assume that fishing activities decreased - although not completely ceased - during the lockdown, causing a decrease in mortality due to harvest and by-catch and perhaps resulting in an increased food source for sea turtles. Unfortunately, this can only be hypothesized, since it is not possible to accurately assess the scale of fishing activities in Cape Verde during these years, although a decline in fishing activity was documented for other Northwest African countries, such as Morocco, due to its serious impact on fish processing industries (World Bank, 2023).

Another interesting outcome resulted from the analysis is that 69.53% of the 21,580 tagged females has been encountered nesting only one time in the 11-year period (Fig. 9). Of course, this result could be due to a limitation in the monitoring program - perhaps they did nest other times but have not been monitored - and certainly this is the case for some of them. However, the fact that a substantial number - 15,005 turtles – were not seen nesting at JB a second time may also indicate either a lower nest-site fidelity than initially assumed or that they nested on immediate adjacent beaches. It is important to keep in mind that JB Beach itself extends for only 5 km and that the adjacent beaches of Ervatão, Ponta Cosme and Coral Velho in the Sea Turtle Natural Reserve are also hosting important numbers of nesting females - a comparative analysis would therefore be required.

Similarly, the results illustrated in Figure 10 indicate that the 73.5% of the total monitored females has only been encountered once at JB. This outcome, together with the one mentioned above, could suggest a third hypothesis and be a clear proof of the high mortality among the population. Some of the turtles might, of course, have been missed during monitoring or might have nested in other adjacent beaches, but 15,863 turtles are a notable number that requires other possible explanations. Mortality in the nesting area in Cape Verde decreased but it is still caused by fishing and hunting activities not on the beach during oviposition but in open waters away from any possible controls on fishing boats. Turtle meat is still consumed by a small part of tourists and locals, even if sea turtles' capture and consumption has been declared illegal since years ago. However, mortality is also related to population density, as higher densities can lead to increased competition, predation, or disease transmission, ultimately resulting in higher mortality rates.

#### 4.1.2. Number of Nests (NN) & Inter-Nesting Interval (INI)

The results emerging from the analysis of the average number of nests laid by the same individual within a nesting season must be interpreted with caution due to possible errors during data collection. It is important to acknowledge that the monitoring program only records a subset of the total nesting population, as nocturnal surveys monitor only a part of the actual nesting events. Each one of the three sectors of JB is patrolled by one team at the time. Therefore, concomitant nesting events taking place on opposite ends of the sector may be missed out. The percentage of turtles monitored relative to the total number of turtles emerging on the beach each night can only be estimated. It can be estimated that during the early morning inspections - when the nests laid overall during the night are identified - an average between 60 and 110 nests per sector can be counted. Moreover, during the night shifts, usually, an average of 20 to 35 turtles can be monitored, depending on the time in the season and on the intensity of nesting activities. Therefore, we can estimate that approximately an average of 30% of the total number of turtles emerging during the peak season are being recorded.

With this in mind, we can conclude that the results from the analysis of the average NN per season are conservative estimates inherent to the monitoring program. This fact was also reflected in the second analysis conducted by including only the females with a higher number of nests per season: the obtained result of 4.11 nests laid on average per female and season might be more realistic.

Similar considerations must be taken into account when observing the outcomes of the INI analysis. Figure 14 shows that most of the females exhibit average INIs consistent with previous studies, with intervals >28 days, between 14-21 days and between 7-14 days being the most common. However, some anomalies exist. Long INIs (>28 days) are unexpected, as *C. caretta* typically completes a reproductive cycle within a defined nesting season. Two are the plausible explanations: either females laid additional nests on adjacent beaches, leading to gaps in recorded nesting events, or some individuals were overlooked in JB due to observational limitations, given the logistic challenges of tracking every individual emerging on the beach.

Extremely short intervals ( $x = 1$ ) are also likely resulting from errors in data collection (same nest recorded again after midnight). In fact, the physiological process of follicle maturation requires time and an ongoing reproductive investment in terms of energy and nutrients even after the arrival at the nesting beach (Bruno et al., 2025), making such brief intervals unlikely. Similarly, the average interval of  $1 < x \leq 7$  days is rare in the literature, raising the possibility of either a misclassification of PIT tags or a misinterpretation of nesting activity. Given the difficulties deriving from the night patrolling, errors are likely to happen, although considering the long span of the monitoring program and the observations included in the database, these errors are likely low. However, after accounting for potential errors in data collection, the possibility that such short intervals ( $1 < x \leq 7$ ) may be real should also be evaluated. Based on field observation, it may be possible that some turtles only laid part of the eggs and then returned few days later to finish laying therefore, the two observed events may be part of the same nest. Another explanation for a shorter INI may be found in a possible higher availability of food and nutrients, or other favorable environmental conditions such as water temperature, that might have accelerated the finalization of the follicle maturation process and shorten the inter-nesting intervals (Hays et al. 2002). This finding contrasts with reported inter-nesting intervals in Loggerhead turtles, which typically range between 10 and 17 days (Miller, 1997; Hays et al., 2002; Broderick, 1999; González et al., 2020; Varo-Cruz, 2010) and would require additional investigation to corroborate it.

#### 4.1.3. Remigration Interval (RI)

The RI analysis also revealed some unexpected results and some anomalies if compared to literature, where the RIs are usually around 2 and 3 years (Miller, 1997; Schroeder et al., 2003; Marcovaldi et al., 2010; González et al., 2020; Varo-Cruz, 2010). Generally, remigration intervals can provide important information about reproductive investment and survival. The results reported in Figure 16, indicating that more than 90% of the 19,462 nesting females have not been seen nesting in JB Beach in a second season. This might suggest a high mortality among the population. Since mortality in Cape Verde decreased notably, this could probably be attributed to the risks they face in the foraging areas on the Northwest African coast, such as Mauritania, where bycatch and direct harvesting by local fisheries remain serious threats (Mestre et al., 2025).

RI analysis also indicated that some individuals returned to nest after just one year ( $RI = 1$ ). Although the most common RIs were 2 and 3 years (Fig. 17), the 3.09% of the 1780 females included in the RI analysis nested in consecutive years at least once. Of these 55 turtles, 4 of them exhibited the same RI pattern a second time during the 11-years period. In the literature, consecutive-year nesting is rarely documented (Broderick 1999), as females typically require extended foraging periods to replenish energy reserves before undertaking the long reproductive migration again. This outcome, besides representing a novel finding, may also suggest distinct characteristics of this sub-population compared to others previously studied.

The presence of 1-year RIs in our dataset could indicate favorable feeding conditions in nearby waters, allowing some turtles to accumulate sufficient resources within a short period. Another explanation could be that certain individuals undertake shorter migration distances than others within the same populations or than other sub-populations. Loggerhead turtles nesting in Cape Verde tend to be either open ocean or neritic foragers, approaching the West African coast from Mauritania and Senegal to as far south as Sierra Leone (Hawkes et al., 2006). Most likely the length of these different migration routes affects the duration of their RI. Furthermore, certain turtles could even remain in Cape Verdean waters once the nesting season is over, which would certainly reduce energy expenditure, enabling more frequent nesting. Cape Verde as foraging area is not common, probably due to the lack of sufficient food availability, but for a small fraction of the population food availability might be sufficient. Another hypothesis is that certain females may remain in Cape Verde due to diseases or injuries preventing them from undertaking longer migrations. Investigating the presence of amputations among these nesting females could provide further insights into these unusual remigration patterns.

Another hypothesis possibly explaining short RIs is a difference in size among individuals, which would influence the time of energy accumulation and energy use. Within a Japanese population, for example, smaller females have been shown to have longer RI than larger females (Hatase & Tsukamoto, 2008) due to differences in energy budgets and food requirements. Again, alimentation zone can play here a crucial role considering the differences in the foraging areas. Within the studied *C. caretta* sub-population, it has been shown that adults follow two different foraging strategies and that this is linked to body size, with smaller individuals foraging in open waters and larger ones in coastal waters (Hawkes et al., 2006).

These findings should be interpreted with caution, since even if some females are exhibit shorter RIs, they may probably not be able to always sustain consecutive years of nesting. There might be special years when the RIs are lower, as potentially impacted by environmental factors such as sea temperature and, consequently, availability of resources. Years with higher food availability may lead to shorter RIs.

Ultimately, the variability in RIs could be a possible explanation of the fluctuations observed in nesting activity, where peak years such as 2018 and 2021 were followed by a decrease in the number of nesting females and, consequently, of nests. Since most of the females do not undertake migrations in consecutive years, most of those which nested in 2021, for example, did not return in 2022.

Overall, remigration intervals reflect the effort, the high-energy demand and the risks that reproductive migrations represent for Loggerheads. Although a small fraction of the tagged females demonstrated to be able - for several possible reasons - to sustain consecutive-years nesting the most common RIs remain 2 and 3 years.

#### **4.2. Criticisms and Limitations**

Limitations relevant to this study stem from the monitoring efforts conducted at João Barrosa Beach and the data collection process, as well as from the high uncertainty derived from the inherent challenges of studying marine wildlife, where continuous observation of animals is not possible. As previously discussed, potential errors may have arisen from duplicate records - where some nests were counted twice - or from missed nests that were not identified and recorded during the morning inspections. Overall, these opposing sources of error may, to some extent, compensate each other resulting in a relatively balanced estimation of the total number of nests.

Regarding monitoring, the high level of uncertainty associated with this type of study must be acknowledged, particularly due to unobserved turtles. On a high-activity beach such as João Barrosa, it is impossible to monitor all turtles emerging during the night. The extensive area covered, coupled with a limited number of monitors and volunteers, significantly impacts data collection. Many females have been tagged since the beginning of the monitoring program, but data accuracy varies among individuals, leading to a likely underestimation of the total nesting activity occurring at JB. It is, in fact, estimated that only about one-third of the nesting turtles are observed, leaving much of the biology and Behavior of these elusive reptiles still unknown.

Another limitation is represented by the restricted space and time period of the analysis, confined to a 5 km-long beach and to a 11-year dataset. A more extensive database spanning several decades would provide a stronger foundation for assessing nesting patterns such as remigration intervals and the associated factors impacting them. Additionally, an inclusive analysis incorporating data collected at adjacent beaches and on other high-nesting activity islands at Cape Verde would allow a more realistic estimation of the nesting parameters.

Ultimately, nesting Behavior of sea turtles is the complex result of various environmental and anthropogenic factors influencing it. It is an interaction between many different causes, such as variation in sea temperature, food supply, changes in predation pressure or the access to undisturbed and unpolluted nesting sites. They may all contribute to shifts in the nesting parameters.

#### **4.3. Implications of the Study and Future Research Directions**

Overall, the study offers an insight into the population trends over more than a decade. On the one hand, recovery trends have been noted among the population nesting at JB, but cautious interpretation is needed, since the increase can be caused by multiple factors. This could also be a result of the conservation program implemented over the last years by associations like Bios CV, and the establishment of the Sea Turtle Natural Reserve in the south-east part of the island. This aspect can only emphasize the importance of increasing habitat protection, especially for critical nesting sites such as João Barrosa. Furthermore, it underlines the need of implementing integrated monitoring to facilitate data sharing among the conservation associations operating on the island

and across the archipelago. Focusing solely on one site, like in this case on João Barrosa, limits our understandings and can compromise the findings and might lead to misinterpretation.

On the other hand, the results highlighted a conservation concern extending beyond the nesting beaches. A striking observation was the high proportion of tagged females that have not been encountered for a second time at JB Beach within the monitored period (Fig. 10). While this outcome could have partly resulted from a nest-site shifting to adjacent areas or from missed recordings, it may also suggest a high mortality among adults, considering that thousands of tagged females have not been seen returning (73.5%). Given the notable decrease in Loggerhead mortality on land at Cape Verde over the past few decades – mainly thanks to the ongoing conservation programs implemented across the entire country – the suspected high mortality may be potentially occurring during migration or at foraging grounds.

One probable hotspot for such mortality is the foraging area off the Mauritanian coast, an upwelling region characterized by high productivity but also exposed to intense fishing activity, that represent a severe threat for sea turtles foraging there. Beside pollution and intentional harvest, they face significant threats from bycatch, with some of the potentially highest global bycatch rates reported in gillnets, handlines and longline fisheries, estimated between 14,000 and 90,000 turtles per year per country (de la Hoz Schilling et al., 2023).

Additionally, the current socio-economic situation in Mauritania, including widespread poverty and food insecurity, may contribute to the continued exploitation of sea turtles as a food source, especially among the fishermen living in poor conditions and where alternative protein sources are limited. These factors make the Northwest African coast one of the most dangerous regions for the adult turtles of the Northeast Atlantic sub-population.

While conservation programs, enhancing the protection of the nesting beaches, have notably improved over the last years across all the Cape Verdean islands - particularly through land-based efforts and eco-tourism - ocean waters remain largely uncontrolled, and fishing activities keep representing a threat. Strengthening marine conservation in nesting grounds is, therefore, of vital importance, however, not sufficient. Adult mortality is alarming, as mature females are vital for the recovery of this endangered sub-population. Conservation funding must, therefore, be addressed towards the identified foraging grounds on the Northwest African coast, like Mauritania, in order to guarantee the long-term viability of the NEA sub-population.

## **5. Conclusion**

The study investigated the nesting Behavior of Loggerhead sea turtles within the endangered Northeast Atlantic sub-population nesting in Cape Verde, focusing on three nesting parameters: Number of Nests (NN), Inter-Nesting Interval (INI) and Remigration Interval (RI). The analyzed database included more than 30,000 observations of nesting events recorded over an 11-years period at João Barrosa (JB) Beach, on Boa Vista Island, representing the first time-series dataset with >10 years of continuous data for this RMU collected on this island.

Data analysis revealed that, although most of the 19,462 tagged nesting females have been observed depositing only one nest on average - likely due to the limitations in monitoring all nesting events – some individuals nested up to five or six times within a single nesting season. Assuming that many nesting events were missed, a more accurate average was calculated based on the females monitored more consistently, resulting in an average number of nests of 4.11 per female/season.

Inter-nesting interval analysis revealed that, in line with previous findings, the majority of subsequent nests were laid between 7 and 14 days after the previous one, where intervals exceeding 28 days were excluded, as they likely reflect gaps in monitoring rather than true biological patterns. An interesting outcome was that some of the 3,462 nesting females included in the INI analysis - those observed laying at least two nests within the same season - showed an average INI between one and seven days ( $1 < x \leq 7$ ), a pattern rarely documented in the literature. After accounting for potential errors in data collection, shorter intervals may still be plausible, suggesting that variations in environmental and biological factors might contribute to intra-population differences in oviposition timing.

Among the 1,780 nesting females included in the RI analysis, monitored in at least a second nesting season, the findings revealed a predominant 3-year RI, followed by a 2-year interval in line with previous studies. However, an interesting and rarely documented finding was the occurrence of a shorter RI (RI=1), indicating that a small fraction of females in this sub-population (3.09%) returned to nest in consecutive years. These findings indicate intra-population variability in remigration intervals, also suggesting that environmental or energetic factors, such as foraging area, availability of food and energy storage, might influence the frequency with which females undertake the long and energy-demanding reproductive migrations.

The data also showed that nesting activity followed an increasing trend over the last years, suggesting an apparent recovery in the nesting population, although data must be interpreted with caution. Several factors could be contributing to the increasing number of nesting females, and for a more accurate understanding and estimation of the population trends, integrated monitoring - including data from other conservation associations - would be recommended. A concerning finding is the ratio of recaptured turtles across the years. Within the same nesting seasons, the number of newly tagged individuals was generally higher than the recaptured ones, suggesting a high turnover in the nesting population. Furthermore, the fact that 73.5% of the 21,580 females tagged in total have not been observed again throughout the entire monitoring period suggest a high mortality among the adult individuals. Since conservation programs have been increasingly implemented in Cape Verde Islands over the last years, high mortality rates may be assumed in foraging grounds along the Northwest coast of Africa, in countries such as Mauritania. By-catch rates in this region are among the highest globally reported. This suggests an urgent need for conservation funding directed towards these countries, where poverty and the impacts of climate change are putting significant pressure on local communities

Overall, these results contribute to a more detailed understanding of the reproductive ecology of the NEA sub-population in Cape Verde and reinforce the value of long-term monitoring programs. They suggest variability within individual reproductive strategies and serve as a reference point for future comparisons, especially in the context of changing environmental conditions. They indicate that the conservation of this population cannot rely solely on efforts in the nesting grounds but should involve coordinated protection across the foraging area. For effective regional conservation of this endangered migratory species, it is necessary to expand scientific and conservation efforts to these under-monitored regions along the Northwest African coast, particularly in Mauritania, to mitigate the risks that this endangered sub-population is currently facing.

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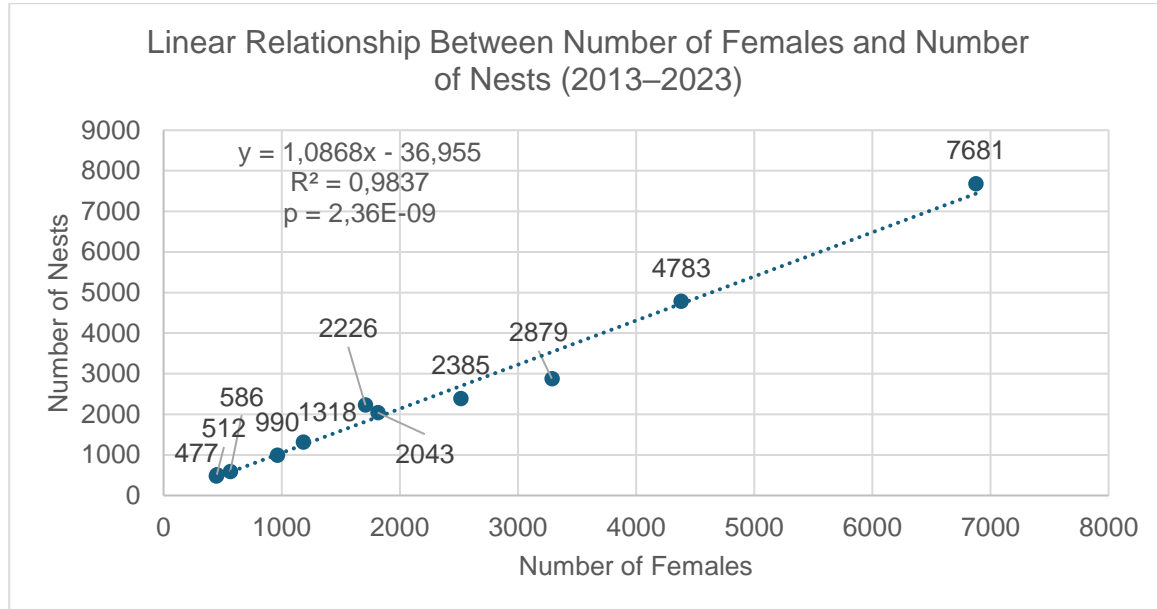
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## Appendix

### Annex 1 - Linear relationship between number of females and number of nests at João Barrosa Beach (2013–2023)

Scatterplot with regression line illustrating the positive correlation between the number of females and the total number of nests recorded each season at JB Beach from 2013 to 2023. The regression equation is  $y = 1.09x - 36.95$ , with  $R^2 = 0.98$  and  $p < 0.001$ , suggesting that, on average, each female contributed to approximately 1.09 nests per season.



### Annex 2 – PIT tags of females with average INI between one and seven days ( $1 < x \leq 7$ )

N	PIT TAG	DATE of NEST	INTERVAL BETWEEN NESTS (DAYS)	INTERVAL CATEGORY	Average INI per PIT TAG
1	941000020399155	03/08/2020	2	1 < x ≤ 7 Days	2,00
	941000020399155	05/08/2020			
2	941000020401559	19/09/2019	7	1 < x ≤ 7 Days	7,00
	941000020401559	26/09/2019			
3	941000022742171	01/09/2018	4	1 < x ≤ 7 Days	4,00
	941000022742171	05/09/2018			
4	941000026575240	15/08/2021	7	1 < x ≤ 7 Days	7,00
	941000026575240	22/08/2021			
5	941000026576408	17/09/2021	2	1 < x ≤ 7 Days	2,00
	941000026576408	19/09/2021			
6	941000026576642	15/09/2021	2	1 < x ≤ 7 Days	2,00
	941000026576642	17/09/2021			
7	941000026578339	07/08/2021	2	1 < x ≤ 7 Days	2,00
	941000026578339	09/08/2021			
8	941000026578360	07/08/2021	3	1 < x ≤ 7 Days	3,00
	941000026578360	10/08/2021			
9	941000026580569	10/09/2021	7	1 < x ≤ 7 Days	7,00
	941000026580569	17/09/2021			
10	941000026580743	31/08/2021	5	1 < x ≤ 7 Days	5,00
	941000026580743	05/09/2021			
11	941000026582859	21/08/2021	4	1 < x ≤ 7 Days	4,00

	941000026582859	25/08/2021			
12	941000026585412	19/08/2021	2	1 < x ≤ 7 Days	2,00
	941000026585412	21/08/2021			
13	941000026585694	24/09/2021	5	1 < x ≤ 7 Days	5,00
	941000026585694	29/09/2021			
14	941000026590974	08/10/2021	2	1 < x ≤ 7 Days	2,00
	941000026590974	10/10/2021			
15	941000026593432	27/09/2021	2	1 < x ≤ 7 Days	2,00
	941000026593432	29/09/2021			
16	941000026593782	06/09/2021	4	1 < x ≤ 7 Days	4,00
	941000026593782	10/09/2021			
17	941000026593859	09/09/2021	2	1 < x ≤ 7 Days	2,00
	941000026593859	11/09/2021			
18	941000027087540	02/09/2022	11	7 < x ≤ 14 Days	6,50
	941000027087540	13/09/2022	2	1 < x ≤ 7 Days	
	941000027087540	15/09/2022			
19	941000027091674	17/08/2022	2	1 < x ≤ 7 Days	6,50
	941000027091674	19/08/2022	11	7 < x ≤ 14 Days	
	941000027091674	30/08/2022			
20	977200009200882	08/08/2017	4	1 < x ≤ 7 Days	4,00
	977200009200882	12/08/2017			
21	977200009208091	22/08/2017	1	x=1	6,50
	977200009208091	23/08/2017	12	7 < x ≤ 14 Days	
	977200009208091	04/09/2017			
22	981020000348260	24/09/2017	7	1 < x ≤ 7 Days	7,00
	981020000348260	01/10/2017			
23	981098108227419	10/09/2020	6	1 < x ≤ 7 Days	6,00
	981098108227419	16/09/2020			
24	981098108229388	02/07/2021	5	1 < x ≤ 7 Days	5,00
	981098108229388	07/07/2021			
25	981098108229511	02/07/2021	4	1 < x ≤ 7 Days	4,00
	981098108229511	06/07/2021			
26	981098108230695	31/07/2021	2	1 < x ≤ 7 Days	2,00
	981098108230695	02/08/2021			
27	981098108231794	22/09/2020	3	1 < x ≤ 7 Days	3,00
	981098108231794	25/09/2020			
28	981098108247321	14/07/2021	2	1 < x ≤ 7 Days	2,00
	981098108247321	16/07/2021			
29	981098108247909	15/07/2021	7	1 < x ≤ 7 Days	7,00
	981098108247909	22/07/2021			
30	146518663A	05/07/2016	2	1 < x ≤ 7 Days	4,00
	146518663A	07/07/2016	6	1 < x ≤ 7 Days	
	146518663A	13/07/2016			

Annex 3 – Average IMI of the nine females with more returns recorded

PIT TAG	DATE of RETURNS	INTERVAL in DAYS	Avarage IMI	PIT TAG	DATE of RETURNS	INTERVAL in DAYS	Avarage IMI	
977200007415015	30/06/2013	2	8,13	941000022737610	12/07/2018	2	12,83	
977200007415015	02/07/2013	1		941000022737610	14/07/2018	16		
977200007415015	03/07/2013	2		941000022737610	30/07/2018	1		
977200007415015	05/07/2013	14		941000022737610	31/07/2018	1		
977200007415015	19/07/2013	2		941000022737610	01/08/2018	1		
977200007415015	21/07/2013	14		941000022737610	02/08/2018	56		
977200007415015	04/08/2013	14		11,83	941000022737610	27/09/2018		10,17
977200007415015	18/08/2013				941000022743565	02/08/2019	1	
977200007415015	09/07/2018	16			941000022743565	03/08/2019	1	
977200007415015	25/07/2018				941000022743565	04/08/2019	1	
977200008325774	19/07/2014	17	941000022743565		05/08/2019	1		
977200008325774	05/08/2014	14	941000022743565		06/08/2019	44		
977200008325774	19/08/2014	13	12,20		941000022743565	19/09/2019	13	12,55
977200008325774	01/09/2014	1			941000022743565	02/10/2019		
977200008325774	02/09/2014	13			152109661A	06/08/2017	2	
977200008325774	15/09/2014	13			152109661A	08/08/2017	11	
977200008325774	28/09/2014			152109661A	19/08/2017	13		
977200008329825	02/07/2014	7		152109661A	01/09/2017	25		
977200008329825	09/07/2014	36		152109661A	26/09/2017	649		
977200008329825	14/08/2014	14	7,83	152109661A	07/07/2019	14	12,50	
977200008329825	28/08/2014	3		152109661A	21/07/2019	16		
977200008329825	31/08/2014	1		152109661A	06/08/2019	2		
977200008329825	01/09/2014			152109661A	08/08/2019	14		
977200009094490	29/06/2017	16		152109661A	22/08/2019	13		
977200009094490	15/07/2017	1		152109661A	04/09/2019	12		
977200009094490	16/07/2017	15		152109661A	16/09/2019	664		
977200009094490	31/07/2017	1	9,83	152109661A	11/07/2021	16	10,87	
977200009094490	01/08/2017	13		152109661A	27/07/2021			
977200009094490	14/08/2017	1		981098108230181	12/07/2021	5		
977200009094490	15/08/2017			981098108230181	17/07/2021	17		
977200009208615	22/07/2017	13		981098108230181	03/08/2021	16		
977200009208615	04/08/2017	1		981098108230181	19/08/2021	32		
977200009208615	05/08/2017	4		981098108230181	20/09/2021	2		
977200009208615	09/08/2017	13	10,87	981098108230181	22/09/2021	3		
977200009208615	22/08/2017	2		981098108230181	25/09/2021			
977200009208615	24/08/2017	26						
977200009208615	19/09/2017							



Annex 4 – Photos from fieldwork at João Barrosa Beach. Credits to E. Davò. Edited with Canva.com

