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**The effect of nest abundance of Loggerhead turtles on  
the nest predation rate of ghost crabs in Cabo Verde**



**UNIVERSIDADE DO ALGARVE**

Faculdade de Ciências e Tecnologia

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**Mestrado em Biologia Marinha**

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2022

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Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

Kaja Lena Boner

## **Title**

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Kaja Lena Boner

## **Abstracts**

### **English**

The Loggerhead sea turtle (*Caretta caretta*) is facing intense nest predation globally. The subpopulation nesting on the Cabo Verde Archipelago, which is categorized as Endangered on the IUCN List, has been encountering high predation rates caused by ghost crabs (*Ocypode cursor*), the main predator on these oceanic islands. This study investigates the effect of nest abundance of Loggerheads on nest predation by ghost crabs on Boa Vista, Cabo Verde, from 2013 to 2021. Boa Vista hosts around 60% of the Loggerhead nests in Cabo Verde which is one of the world's largest Loggerhead rookeries. The nest abundance was recorded during night patrol and daily beach surveys at dawn. The predation of ghost crabs was evaluated using natural Loggerhead nests that were checked daily for any evidence of predation, inundation, erosion, or any other relevant disturbances to the nest. The clutch size of these nests was counted during oviposition and the nests were exhumed after the incubation period to assess the number of hatched, enclosed, and missing eggs. The interannual variability in Loggerhead nests was high, ranging from 1123 to 33496 nests. The nest mortality by crab predation was strongly negatively correlated to the nest abundance. Seasons with a low nest abundance showed high crab predation rates of up to 75%, whereas in seasons with high nest abundance crab predation rates as low as 4% were observed. Higher nest abundance might exceed the capacity to consume sea turtle eggs of the ghost crab population on the studied beach. Through predator satiation caused by high nest abundance, the risk of predation and the extent of the predation may be reduced. The findings give an interesting insight into this predator-prey interaction but also highlight the importance of conservation efforts in reducing predation, especially for areas and seasons with low sea turtle nest abundance.

### **Portuguese**

A tartaruga-cabeçuda (*Caretta caretta*) enfrenta intensa predação de ninhos em todo o mundo. A subpopulação que nidifica no Arquipélago de Cabo Verde, classificada como Ameaçada na Lista da IUCN, tem vindo a encontrar elevadas taxas de predação causadas pelo caranguejo-fantasma (*Ocypode cursor*), o principal predador destas ilhas oceânicas. Cabo Verde está localizado no Atlântico oriental, a cerca de 570 quilómetros da costa ocidental de África. Os caranguejos-fantasma são invertebrados semi-terrestres que habitam praias oceânicas tropicais e subtropicais, em todo o mundo. Na zona entre-marés das praias, escavam tocas profundas, nas quais vivem solitariamente e procuram abrigo durante o dia. Como animais crepusculares

e noturnos, exploram a praia à noite. A dieta omnívora dos caranguejos fantasmas consiste em uma ampla gama de ítems alimentares, incluindo ovos e filhotes de tartaruga, macroinvertebrados e insetos da zona de rebentação, mas também detritos marinhos e restos alimentares de humanos. Os caranguejos-fantasma são predados por uma variedade de répteis, pássaros e mamíferos (por exemplo, guaxinins), mas nenhum desses predadores é encontrado em Cabo Verde.

Este estudo investiga o efeito da predação de ninhos por caranguejos fantasmas na abundância de tartarugas-cabeçudas, na ilha de Boa Vista, Cabo Verde, de 2013 a 2021. Boa Vista hospeda cerca de 60% dos ninhos de tartaruga-cabeçuda em Cabo Verde, sendo uma das maiores colónias desta espécie do mundo. A abundância de ninhos foi registrada durante patrulhamento noturno e levantamentos diários na praia, ao amanhecer. É a soma de ninhos encontrados durante o processo de nidificação à noite e ninhos encontrados com base em pegadas, ao amanhecer. Os dados utilizados para avaliar a predação de caranguejo-fantasma em ninhos de *C. caretta* foram recolhidos através de marcação e monitorização de ninhos naturais. Os tamanhos das ninhadas foram contados durante a oviposição. Durante os levantamentos matinais, todos os ninhos monitorizados foram verificados diariamente para registo de qualquer evidência de predação, inundação, erosão ou qualquer outra perturbação relevante no ninho. A predação por caranguejo-fantasma foi detectada pela presença de buracos circulares próximos dos ninhos. Após o período de incubação, os ninhos foram exumados para avaliar o número de ovos eclodidos, enclausurados e ausentes. Com base nesses valores e nas observações durante os períodos de incubação, foi calculada a mortalidade ocorrida no ninho por predação de caranguejos.

A variabilidade interanual no número de ninhos de tartaruga-cabeçuda foi alta, variando de 1123 a 33496 ninhos. A mortalidade média observada nos ninhos variou de 36,49% a 92,77%. A predação por caranguejos foi negativamente correlacionada com a abundância de ninhos. Foram observadas épocas de baixa abundância com taxas de predação por caranguejos de até 75 %, enquanto nas épocas do ano de alta abundância foram observadas taxas de predação por caranguejos tão baixas quanto 4%. O número de ninhos predados está fortemente correlacionado com o número de ninhos e a percentagem de ninhos totalmente predados mostra uma correlação negativa muito forte com o número de ninhos. O maior valor de ninhos predados para o período estudado foi de 90% e o menor valor foi de 61%. O valor máximo de ninhos totalmente predados foi de 61% e o mínimo foi de 5%. O número médio de buracos de

caranguejo variou de 6 a 25 buracos por ninho e mostrou uma forte correlação negativa significativa com a abundância de ninhos.

Maior abundância de ninhos reduz os riscos de predação por caranguejo-fantasma, bem como a extensão da predação. A alta abundância pode exceder a capacidade de consumir ovos de tartarugas por parte da população de caranguejo-fantasma na praia estudada. Devido à saciedade do predador pela alta abundância de ninhos, o risco de predação e a extensão da predação podem ser reduzidos.

A ausência de predadores de caranguejo-fantasma e a boa qualidade da praia podem levar a alta densidade de caranguejo explicando as taxas de predação extremamente altas em locais com baixa abundância de ninhos. A presença de grandes predadores de ovos de tartarugas marinhas nas praias de nidificação mostrou reduzir a predação por caranguejos, noutros locais. Como, aqui, não há predadores além dos humanos, que raramente usam grandes caranguejos como isca, a densidade de caranguejos não é limitada pelo predador. A área de estudo é uma praia remota sem urbanização e com turismo de observação de tartarugas marinhas controlado. O baixo impacto humano e a falta de predadores de caranguejos podem explicar a grande população estável de caranguejo-fantasma na ilha de Boa Vista.

Durante a época de nidificação, as tartarugas marinhas nidificam várias vezes, mas geralmente apenas se reproduzem a cada 2 a 5 anos, raramente nidificando em duas temporadas consecutivas. O intervalo entre dois períodos de nidificação de um indivíduo pode ser influenciado por fatores ambientais, como abundância de alimento. A alta disponibilidade de alimento pode reduzir o intervalo entre duas épocas de nidificação, explicando as épocas com alta abundância de ninhos. A variabilidade interanual dessa abundância pode ser uma estratégia de evitamento de predadores, pois números mais altos de ninhos reduzem o risco de predação. A sobrevivência dos ovos pode ser maior com variabilidade interanual ao invés de igual ao longo dos anos. A variabilidade interanual desta abundância observada neste estudo é relativamente alta. Isso pode ser explicado por um aumento no tamanho da população, pois os quatro maiores valores de abundância foram registrados nos últimos 4 anos do período de estudo.

A predação de ninhos é uma questão desafiadora para a conservação das tartarugas marinhas. Esta pesquisa mostra que a alta abundância de ninhos reduz a mortalidade por predação. Esse

conhecimento pode ser implicado em estratégias de conservação. Em relação à predação de ninhos, o incubatório é uma boa ferramenta para locais com baixa abundância de ninhos, pois a taxa de predação é alta e o impacto de ninhos translocados alto, porém outras estratégias de conservação devem ser discutidas para locais com alta abundância de ninhos, pois a taxa de predação é baixa e o impacto de ninhos translocados é alto. As consequências da taxa de predação para a subpopulação estudada só serão observadas em algumas décadas, pois a idade de maturidade sexual da tartaruga-cabeçuda varia muito entre os indivíduos e é estimada entre 10 e 39 anos. O número reduzido de filhotes devido à predação pode retardar a recuperação dessa população ameaçada.

As conclusões do presente estudo oferecem uma visão interessante da interação presa-predador. Além disso, enfatiza o impacto do caranguejo-fantasmas como predador de ovos de tartaruga-cabeçuda, uma vez que a mortalidade por predação por caranguejo pode atingir 75%. Destaca-se, também, a importância dos esforços de conservação para redução da predação, especialmente em áreas e épocas do ano com baixa abundância de ninhos de tartarugas marinhas.

**Keywords:** Cape Verde; *Caretta caretta*; Ghost crab; Nest abundance; Nest predation



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## **Chapter 1**

### **General introduction**

#### **Sea turtles in Cabo Verde**

The Loggerhead sea turtle (*Caretta caretta*) is globally distributed in subtropical to temperate regions of the Mediterranean Sea and the Atlantic, Indian, and Pacific Oceans (Wallace *et al.*, 2010). One of the largest nesting aggregations of Loggerheads is found in Cabo Verde (S. Martins, Tiwari, *et al.*, 2022). The archipelago of Cabo Verde is located in the Eastern Atlantic, about 570 km off the western coast of Africa. This area is a feeding ground for juvenile Green turtles (*Chelonia mydas*) and Hawksbill turtles (*Eretmochelys imbricata*) (Marco *et al.*, 2011). Olive Ridley (*Lepidochelys olivacea*) and Leatherback turtles (*Dermochelys coriacea*) migrate through the waters of Cabo Verde (López-Jurado *et al.*, 2002), only Loggerhead turtles (*Caretta caretta*) nest in high numbers on the beaches of Cabo Verde (Marco *et al.*, 2011; Marco, Abella, *et al.*, 2012).

#### **Life cycle of *Caretta caretta***

*Caretta caretta*, like all sea turtles and most reptiles, is an oviparous species that digs nests where they lay their eggs (Deeming, 2004). After approximately 50 to 60 days of incubation time, hatchlings emerge from their nest and search their way to the ocean (Rocha *et al.*, 2015; Aguilera *et al.*, 2018). The hatchlings safely reaching the sea start long oceanic migration using major currents (Bolten *et al.*, 1998). After spending several years in the open ocean and reaching sexual maturity, the turtles find their way back to their natal rookery and nest there (Bjorndal, Bolten and Martins, 2000; Bjorndal *et al.*, 2003; Cameron, Baltazar-Soares and Eizaguirre, 2019). The age of sexual maturity for Loggerheads varies greatly among individuals and is estimated to be between 10 and 39 years (Avens and Snover, 2013).

#### **Nesting process**

The general nesting process of Loggerheads includes emerging from the wave wash, ascending the beach, constructing the body pit, digging the egg chamber, followed by oviposition, closing the egg chamber, camouflaging, and returning to the sea (Miller, Limpus and Godfrey, 2003). During the ascend on the beach, Loggerheads are easily disturbed by light, movement, and obstacles (Miller, Limpus and Godfrey, 2003; Taylor and Cozens, 2010; Silva *et al.*, 2017). This can cause a change in direction of the female's path or even the termination of the nesting

attempt (Dodd Jr, 1988; Taylor and Cozens, 2010). Turtles returning to the sea without laying a nest usually return later the same night or during a following night to nest. The majority of turtles that aborted a nest attempt return to the same beach (Limpus, 1985). After finding a suitable nesting spot, the female disperses loose sand with her flippers and constructs a “body pit” (a circular area) by moving her body (Hailman and Elowson, 1992). The turtle uses its rear flippers as shovels to excavate the egg cavity (Schulz, 1975). When the female has finished digging the egg chamber, she starts laying eggs, depositing them singly or in small groups of up to four (Hailman and Elowson, 1992). The clutch size varies among populations and ranges from tenths of eggs to over 100 (Eckert *et al.*, 1999; Tiwari and Bjorndal, 2000). During oviposition, Loggerheads are relatively tolerant to external disturbances and after oviposition, their tolerance even increases (Miller, Limpus and Godfrey, 2003). The nest is closed by filling sand into the egg chamber and compacting it with the rear flippers (Hailman and Elowson, 1992). Before returning to the sea, the turtle moves away from the nest while throwing sand backward with her front flippers (Miller, Limpus and Godfrey, 2003). As a result, the traces of the body pit are not above the egg chamber and the nest is disguised (Hailman and Elowson, 1992). Usually, the nesting process of Loggerheads takes 1 to 2 hours (Hirth, 1980).

### **Nest conditions**

Two factors affecting numerous aspects of embryonic development including embryo growth rate and hatching success are nest temperature and moisture content (McGehee, 1990; Mortimer, 1990; Ackerman, 1994; Wyneken and Lolavar, 2015). Developmental differences are caused by the interaction of temperature and moisture. Higher water content in the sand results in sand temperatures lower than the temperature of surrounding air (Sifuentes-Romero *et al.*, 2018). The water intake by the eggs is significantly higher on wetter substrates but embryos develop slowly in cooler and more moist sand substrates (Janzen, Ast and Paukstis, 1995; Delmas *et al.*, 2008; Tezak *et al.*, 2020). The successful development of sea turtle embryos is limited to incubation temperatures ranging from 27 to 33 °C (Fisher, Godfrey and Owens, 2014; Ackerman, 2017). The sex determination of sea turtles is temperature-dependent. Embryos incubating at higher temperatures become female and those at lower temperatures become male (Yntema and Mrosovsky, 1982; Mrosovsky *et al.*, 1985; Hewavisenthi and Parmenter, 2000).

## Nesting season on Cabo Verde

Recent studies suggest that the nesting population of Cabo Verde is the biggest globally as the nest abundance is higher than previously estimated and therefore overtaking nesting populations in Florida and Oman (Laloë *et al.*, 2020; Patino-Martinez, Dos Passos, *et al.*, 2022). The nesting season on Cabo Verde starts at the beginning of June and lasts until mid-October (Marco *et al.*, 2012). It is estimated that during this period each female nests between 4 to 6 times with breaks of 14 to 18 days between the nesting activities. The mature females usually breed every 2 to 5 years, rarely nesting in two consecutive seasons (Marco *et al.*, 2018). The main nesting activity on Cabo Verde occurs on a total of about 40 kilometers of beach length (Marco *et al.*, 2011). The most important Cabo Verdean Island for nesting is Boa Vista with around 60% of all nesting activity in Cabo Verde (Marco *et al.*, 2021). Boa Vista is the most eastern island of Cabo Verde and has a reserve for turtles (Reserva Natural das Tartarugas) located on the southeastern coast established to protect the nesting females. The Reserva Natural das Tartarugas possibly holds the highest nest density of *C. caretta* globally with segments reaching over 800 m in length and more than two nests per meter (Marco, Abella, *et al.*, 2012). Data for this study was collected on the nesting beach of João Barrosa, located on the southeastern coast of Boa Vista, for the nesting seasons from 2013 to 2021. This nesting beach is 5 km long and located in The Reserva Natural das Tartarugas (S. Martins, Patrício, *et al.*, 2022).



**Fig. 1.1** Loggerhead tracks on the nesting beach João Barrosa, Cabo Verde (photo by Adolfo Marco).

## **Threats to turtles**

Sea turtles in Cabo Verde and around the globe are facing numerous anthropogenic threats. On the IUCN Red List, the species *C. caretta* is categorized as Vulnerable (Casale and Tucker, 2017) while the Northeast Atlantic subpopulation that mainly nests in Cabo Verde is categorized as Endangered (Casale and Marco, 2015). The size as well as the quality of the nesting habitats in Cabo Verde are decreasing due to local construction projects and the growing tourism industry (de Santos Loureiro, 2008). The increasing light pollution along the nesting beaches can deter nesting females from coming ashore to nest and can disorient hatchlings trying to find their way to the sea after hatching (Silva *et al.*, 2017).

In the past, one main threat to Loggerheads on Boa Vista was the illegal killing of nesting females (between 5 and 36% of females nesting per year in the years 2007 to 2009) for meat consumption or trade (Marco *et al.*, 2012; Dutra and Koenen, 2014). Today, these numbers are reduced by 90 to 100% due to the work of four NGOs on Boa Vista (including BIOS CV) (Reischig, Resende and Cordes, 2018). These organizations protect nesting sea turtles by patrolling the beach at night and educating the local population on the importance of sea turtles for Cabo Verde. However, sea turtles are still facing issues including bycatch or direct poaching at sea (Melo and Melo, 2013; S. Martins, Tiwari, *et al.*, 2022).

## **Threats and Predators for nests**

Natural threats causing high egg mortality in the nests on Cabo Verde are high tide flooding (García-Carcel and López-Jurado, 2005), warmer incubation temperatures (Martins *et al.*, 2020), clay accumulation in the sand (Marco, Abella-Perez and Tiwari, 2017), fungus infection with *Fusarium falciforme* and *Fusarium keratoplasticum* (Sarmiento-Ramirez *et al.*, 2014), and nest predation (da Graça *et al.*, 2013).

Flooding-induced mortality of eggs is one of the factors threatening high hatching success of Loggerhead sea turtles (García-Carcel and López-Jurado, 2005; S. Martins, Patino, *et al.*, 2022). Freshly laid eggs and eggs nearly hatching are particularly vulnerable to flooding. Inundation exceeding a duration of 6 hours regardless of the incubation phase causes disturbances of gas concentrations and osmotic gradients in the egg chamber which can lead to high mortality of embryos (Limpus, Miller and Pfaller, 2020). Climate change plays a major role as the rising temperatures cause seawater to expand and ice over land to melt, leading to a rising sea level. This phenomenon in addition to, and in part interconnected with, coastal flooding is concerning,

especially when considering that flooding significantly decreases hatching success (García-Carcel and López-Jurado, 2005; Limpus, Miller and Pfaller, 2020).

The changing climate with increased temperatures also directly impacts egg mortality as it has been shown that higher incubation temperatures within the temperature range of successful embryo development cause higher embryo mortality (Martins *et al.*, 2020). An increase in global temperature supports the female-biased sex ratio in the sea turtle populations around the world which consequently will cause a variety of problems (Mrosovsky and Provancha, 1992; Hays, Mazaris and Schofield, 2014). Similarly, a highly feminized sex ratio of 84% female hatchlings has been estimated for the nesting aggregation of Loggerhead sea turtles in Cabo Verde (Tanner *et al.*, 2019). Moreover, an increase in global temperature also increases the risk of high egg mortality due to lethal incubation temperatures (Matsuzawa *et al.*, 2002; Bladow and Milton, 2019).

Eggs laid in substrates rich in clay and silt have shown higher mortalities due to the dehydration of the eggs which can disrupt embryonic development resulting in the death of the embryo (Marco, Abella-Perez and Tiwari, 2017). Along with extracting nutrients, another threat absorbing moisture from the eggs are roots of vegetation on the beach (Witherington, 1986; Hannan *et al.*, 2007).

Infections with fungal pathogens such as *Fusarium falciforme* and *Fusarium keratoplasticum* are major threats to nests of *C. caretta* as the optimal growth temperature of the fungi overlaps with the optimal incubation temperature for the eggs (Sarmiento-Ramirez *et al.*, 2014). These two pathogenic species cause embryonic mortality rates of up to 90%. *F. falciforme* and *F. keratoplasticum* are particularly threatening since they showed higher embryonic mortality rates in nests vulnerable environmental stressors like tidal inundations or contents of clay/silt (Sarmiento-Ramirez *et al.*, 2014).

As a result of low risks for predators and little energy requirement to locate and prey upon eggs, nests are a favored resource as they additionally provide beneficial nutrients (Leighton, Horrocks and Kramer, 2009). Globally, the most important nest predators are carnivore mammals like raccoons (*Procyon lotor*) and ghost crabs (*Ocypode* spp.) (Barton and Roth, 2008; Pheasey *et al.*, 2018; Butler *et al.*, 2020).

Raccoons are often removed from nesting beaches by authorities to reduce egg mortality (Engeman *et al.*, 2006, 2010). Ghost crabs also feed upon the nests of *C. caretta* but are also preyed on by raccoons. A study by Barton and Roth (2008) conducted in Florida discovered that egg predation rates by raccoons and ghost crabs combined are highest when the abundance of raccoons was lowest, and the abundance of ghost crabs was highest. The results of this study indicate that raccoons limit ghost crab density and therefore, the removal of raccoons can increase ghost crab abundance which can result in increased Loggerhead turtle egg mortality (Barton and Roth, 2008).

The main nest predator observed on the nesting beaches of Boa Vista is the ghost crab species *Ocypode cursor* (Marco *et al.*, 2015). Contrary to Florida, no native mammals preying on turtle eggs exist in Cabo Verde, although feral cats and dogs sometimes predate on turtle nests (Marco *et al.*, 2011). Apart from preying on the eggs, ghost crabs also prey on hatchlings emerging from the nest on their way to the ocean (Erb and Wyneken, 2019; Martins, Sierra, *et al.*, 2021).



**Fig.1.2** Ghost crabs in the intertidal zone of nesting beach, Cabo Verde (photo by Adolfo Marco).

### **Life cycle of ghost crabs**

Ghost crabs (*Ocypode* spp.) are semi-terrestrial invertebrates inhabiting tropical and sub-tropical sandy ocean beaches worldwide (Dahl, 1952; Hedgpeth, 1957). They have a planktonic larval stage followed by a transformation into a permanently terrestrial animal (Diaz and

Costlow, 1972). Ghost crabs are considered great bio-indicators of beach quality as they are sensitive to anthropogenic factors like humans compacting sand by trampling (Schlacher, de Jager and Nielsen, 2011). Even though ghost crabs breathe oxygen, water is needed to generate and maintain a humid environment for their gills (Weinstein, Full and Ahn, 1994). In the intertidal zone of the beaches, they excavate deep burrows, in which they live solitary and seek shelter during the warm daytime (Schuchman and Warburg, 1978). As crepuscular and nocturnal animals, they explore the beach at night. Larger individuals advance to the drier parts of the beach, whereas smaller crabs stay closer to the ocean (Strachan *et al.*, 1999; Tiralongo *et al.*, 2020). These crustaceans are fast on land and have an astute sense of smell, sight, and hearing (Schlacher, 2014). The omnivorous diet of ghost crabs includes preying on turtle nests and hatchlings and feeding on carrion and food remains of humans (Trott, 1999; Tiralongo *et al.*, 2020). Furthermore, ghost crabs are preyed on by a variety of reptiles, birds, and mammals (e.g. raccoons) (Hughes, Hughes and Smith, 2014). Due to their variety of roles as prey, predators, scavengers, and bioturbators, ghost crabs display outstanding trophic plasticity and are a key link in sandy beach food webs (Schlacher, 2014).



**Fig. 1.3** Loggerhead nest preyed by ghost crabs (picture by Adolfo Marco).

A study by Marco *et al.* (2015) investigated patterns and extent of ghost crab predation on Loggerhead turtle nests on six beaches of Boa Vista. The results showed significant variations in egg mortality between beaches. The average egg mortality was 70% and one main cause for this high egg mortality was nest predation by ghost crabs, preying more than 98% of nests at



least once during the entire incubation period. On the nesting beach João Barrosa, ghost crabs predated an average of 54.5% of eggs in nests monitored. This research showed the highest predation risk for *C. caretta* nests by ghost crabs at the end of the incubation period. After the 45th day of incubation, more than 80% of the overall predation occurred.

### **Work of NGOs on Cabo Verde/ Conservation strategies against crab predation**

The aims and priorities of the NGOs are to protect the nesting females, nests, and hatchlings by monitoring the beach from sunset until morning (Marco, Abella Pérez, *et al.*, 2012). The monitoring prevents the capture and poaching of nesting females as well as disturbances by ecotourism activities on the beach (Reischig, Resende and Cordes, 2018; Marco *et al.*, 2021). By controlling the turtle watching tourism, its negative impact is reduced and has shown to not affect the turtle reproduction on Cabo Verde (Marco *et al.*, 2021). Furthermore, lost females or those incapable of returning to the sea due to being stuck are rescued. Additionally, the NGOs protect the nests and hatchlings from disturbances and destruction by natural threats (Marco *et al.*, 2011). Another important aspect of the work of NGOs is raising awareness as well as conducting research studies with the goal to protect biodiversity and produce scientific bases of management (Marco, Abella Pérez, *et al.*, 2012; Marín-Capuz and Menéndez Blázquez, 2021).

One conservation strategy to tackle the problem of high ghost crab predation is translocating nests to hatcheries (Martins, Ferreira-Veiga, *et al.*, 2021). Hatcheries are fenced areas preventing nesting females and ghost crabs from entering. The mature females are denied access to prevent damage to the incubating nests as they dig up sand during their nesting process. Additionally, hatcheries are built on higher ground on the nesting beach to avoid flooding (Eckert *et al.*, 1999). Since especially nests at high risk of being flooded are translocated, another main cause for high egg mortality, flooding of nests, is being prevented. The hatching success of nests translocated to the hatchery on João Barrosa is significantly higher than *in-situ* nests with mean values between 70 and 85% (Martins, Ferreira-Veiga, *et al.*, 2021). Nevertheless, there are also studies reporting lower hatching success in relocated nests (Ödemir and Türkozan, 2006; Ahles and Milton, 2016). This could partly be due to incorrect handling during the process of relocation (Abella, Marco and López-Jurado, 2007) or the conditions in the hatchery (Patino-Martinez *et al.*, 2012). Hatcheries as a conservation tool are particularly important in seasons with low nest numbers and natural disasters like hurricanes as they can compensate for lower numbers of hatchlings with higher hatching success (Milton *et al.*, 1994; van Houtan and Bass, 2007; DuBois, Putman and Piacenza, 2020).

### **Identifying species by tracks**

For the differentiation of turtles' tracks by species, it is important to identify the gait type (alternating and simultaneous) and to measure the track width (Pritchard *et al.*, 1983; Eckert *et al.*, 1999). Leatherbacks and Green turtles move their forelimbs and rear limbs simultaneously, leaving symmetrical tracks, whereas Loggerheads, Hawksbills, and Olive Ridleys use an alternating gait leaving asymmetrical tracks (Renous, 1995; Eckert *et al.*, 1999). These turtles move only two flippers forward at once, meaning one front flipper and the rear limb on the opposite side. The track width of Loggerheads is typically 70 to 90cm and the track typically does not show a tail drag mark. The track width of Hawksbills is smaller (70 to 85cm) and often includes a tail drag mark. The track width of Olive Ridley ranges from 70 to 80 cm and the mark of tail drag is lacking or inconspicuous. Tracks of Loggerheads are moderately deep whereas the tracks of Olive Ridley and Hawksbill turtles are shallower. Nevertheless, differentiating between tracks of Loggerheads, Olive Ridley and Hawksbill can be difficult. The appearance of the tracks left by the same turtle can be altered by differences in beach substrate and variation in morphological features (Body size, flipper length) of turtles of the same species which ultimately can produce different track widths. For distinguishing turtle species based on tracks it is important to gain experience and learn to observe the characteristics of the local population of each species (Eckert *et al.*, 1999).

### **Thesis objectives and hypothesis**

This study investigates the effect of the nest abundance of *Caretta caretta* on the nest predation of ghost crabs on Cabo Verde during the seasons from 2013 to 2021. The annual nest abundance on the studied beach is known to fluctuate greatly (Marco *et al.*, 2018); however, it has been increasing overall during the period studied in the present work. The observed predation by ghost crabs on Cabo Verde has been very high (Marco *et al.*, 2015; R. Martins *et al.*, 2022). The interannual variability in nest abundance combined with the results collected from monitored nests from each season is used to analyze the mean nest mortality and especially mean mortality caused by crabs correlated to nest abundance. We hypothesized that the predation rate decreases with increasing nest abundance due to predator satiation, resulting in a lower predation rate while nest abundance is high. The results of this study will be an important contribution to conservation efforts as information on this predator-prey interaction regarding sea turtle abundance is scarce. The same applies to information regarding the predation impact of ghost crabs for environments in which large predators are absent for the crabs, thereby not

controlling the population density of ghost crabs. The findings of this study can help to advance conservation management and efforts for the endangered species *C. caretta*.

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## Chapter 2

# The effect of nest abundance of Loggerhead turtles on the nest predation rate of ghost crabs in Cabo Verde

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**Keywords:** Cape Verde; *Caretta caretta*; Ghost crab; Nest abundance; Nest predation

## **Abstract**

The Loggerhead sea turtle (*Caretta caretta*) is facing intense nest predation globally. The subpopulation nesting on the Cabo Verde Archipelago, which is categorized as Endangered on the IUCN List, has been encountering high predation rates caused by ghost crabs (*Ocypode cursor*), the main predator on these oceanic islands. This study investigates the effect of nest abundance of Loggerheads on nest predation by ghost crabs on Boa Vista, Cabo Verde, from 2013 to 2021. Boa Vista hosts around 60% of the Loggerhead nests in Cabo Verde which is one of the world's largest Loggerhead rookeries. The nest abundance was recorded during night patrol and daily beach surveys at dawn. The predation of ghost crabs was evaluated using natural Loggerhead nests that were checked daily for any evidence of predation, inundation, erosion, or any other relevant disturbances to the nest. The clutch size of these nests was counted during oviposition and the nests were exhumed after the incubation period to assess the number of hatched, enclosed, and missing eggs. The interannual variability in Loggerhead nests was high, ranging from 1123 to 33496 nests. The nest mortality by crab predation was strongly negatively correlated to the nest abundance. Seasons with a low nest abundance showed high crab predation rates of up to 75%, whereas in seasons with high nest abundance crab predation rates as low as 4% were observed. Higher nest abundance might exceed the capacity to consume sea turtle eggs of the ghost crab population on the studied beach. Through predator satiation caused by high nest abundance, the risk of predation and the extent of the predation may be reduced. The findings give an interesting insight into this predator-prey interaction but also highlight the importance of conservation efforts in reducing predation, especially for areas and seasons with low sea turtle nest abundance.

## **Introduction**

Listed as vulnerable by the IUCN, the Loggerhead sea turtle (*Caretta caretta*) is facing a high nest predation rate globally (Trocini *et al.*, 2008; Casale and Tucker, 2015; Marco *et al.*, 2015). Like all sea turtles, *C. caretta* is an oviparous species that digs nests on sandy beaches into which they lay their eggs (Deeming, 2004). During the incubation time of approximately 50-60 days, there are numerous natural and anthropogenic threats to Loggerhead eggs. Natural threats causing high egg mortality include high tide flooding (García-Carcel and López-Jurado, 2005; Limpus, Miller and Pfaller, 2020), warmer incubation temperatures (Bladow and Milton, 2019; Martins *et al.*, 2020), clay accumulation in the sand (Marco, Abella-Perez and Tiwari, 2017), fungus infection (Sarmiento-Ramirez *et al.*, 2014), and nest predation (da Graça *et al.*, 2013; Rocha *et al.*, 2015). Globally, the most important nest predators of Loggerheads are ghost crabs (*Ocypode* spp.) and carnivore mammals such as raccoons and feral dogs (Barton and Roth, 2008; Pheasey *et al.*, 2018; Butler *et al.*, 2020). The high predation rates caused by these predators result in low hatching success, increasing the risk of extinction (Leighton, Horrocks and Kramer, 2011).

Conservation efforts to reduce nest predation include methods protecting the nests, translocations of nests, and predator control/ removal (García, Ceballos and Adaya, 2003; Lei and Booth, 2017; O'Connor *et al.*, 2017). Nest covers such as mesh made of plastic, metal, or bamboo have proven to be an effective predation prevention strategy (Kornaraki *et al.*, 2006; Kurz, Straley and DeGregorio, 2012; Korein *et al.*, 2019). Another approach to reduce nest predation is moving nests to hatcheries, which are fenced areas preventing predators from entering (Eckert *et al.*, 1999). With the correct handling during the translocation and the suitable conditions in the hatchery, the hatching success in hatcheries can be higher than *in situ* (Abella, Marco and López-Jurado, 2007; Patino-Martinez *et al.*, 2012; Martins *et al.*, 2021). Small to mid-size mammals such as raccoons (*Procyon lotor*) are removed from nesting beaches to reduce egg mortality (Engeman *et al.*, 2010). The removal of predators can have unanticipated consequences if interaction among predators is not considered (Barton and Roth, 2008).

For successful conservation, it is important to consider the food web connectivity of the protected areas as predators of sea turtle eggs also prey on other egg predators (Trocini *et al.*, 2008). In Florida, raccoons are often removed from nesting beaches to reduce Loggerhead mortality through predation. Ghost crabs also feed on the nests of *C. caretta* in Florida but are also preyed upon by raccoons. A study by Barton and Roth (2008) discovered that egg predation

rates by raccoons and ghost crabs combined were highest when the abundance of raccoons was lowest, and the abundance of ghost crabs was highest.

Ghost crabs are semi-terrestrial invertebrates inhabiting tropical and sub-tropical sandy ocean beaches worldwide (Dahl, 1952; Hedgpeth, 1957). They have a planktonic larval stage followed by a transformation into a permanently terrestrial animal (Diaz and Costlow, 1972). In the intertidal zone of the beaches, they excavate deep burrows, in which they live solitarily and seek shelter during the warm daytime (Schuchman and Warburg, 1978). As crepuscular and nocturnal animals, they explore the beach at night. Larger individuals then advance to the drier parts of the beach, whereas smaller crabs stay closer to the ocean (Strachan *et al.*, 1999). Ghost crabs are preyed on by a variety of reptiles, birds, and mammals (e.g. raccoons) (Hughes, Hughes and Smith, 2014). The omnivorous diet of ghost crabs consists of a wide range of food items including turtle eggs and hatchlings, swash zone macroinvertebrates and insects but also carrion and food remains of humans (Trott, 1999; Morrow, Bell and Tewfik, 2014).

The main nest predator of *C. caretta* observed on the nesting beaches of Cabo Verde is the ghost crab species *Ocypode cursor* (Marco *et al.*, 2015). Cabo Verde hosts one of the biggest rookeries of *C. caretta* worldwide. Recent studies suggest that the nesting population of Cabo Verde is the biggest globally as the nest abundance there is higher than previously estimated and therefore overtaking nesting population sizes in Florida and Oman (Laloë *et al.*, 2020; Patino-Martinez, dos Passos, *et al.*, 2022). Contrary to Florida, no native mammals preying on turtle eggs exist in Cabo Verde, although feral cats and dogs sometimes predate on turtle nests (Marco *et al.*, 2011). None of the ghost crab predators have been observed on Cabo Verde. However, large crabs are traditionally used as bait to catch carnivorous fish (Marco *et al.*, 2015).

Research conducted on a Hawksbill turtle nesting beach on the Seychelles identified an increase in ghost crab densities with an increasing number of incubating turtle nests (Gane *et al.*, 2021). However, the nesting density on the beach of the Seychelles is distinctly lower than on Boa Vista (Gane *et al.*, 2020). Higher nest density could satiate the predator and result in contradictory findings compared to those obtained on the Seychelles explained by the predator satiation hypothesis. This hypothesis proposes that a brief, extremely high abundance of prey can exceed the capacity of predators to consume them (Donaldson, 1993). Eckrich and Owens (1995) tested the predator satiation hypothesis on nests of Olive Ridley turtles predated by mammals on the first night after oviposition. The comparison of nests deposited by individually

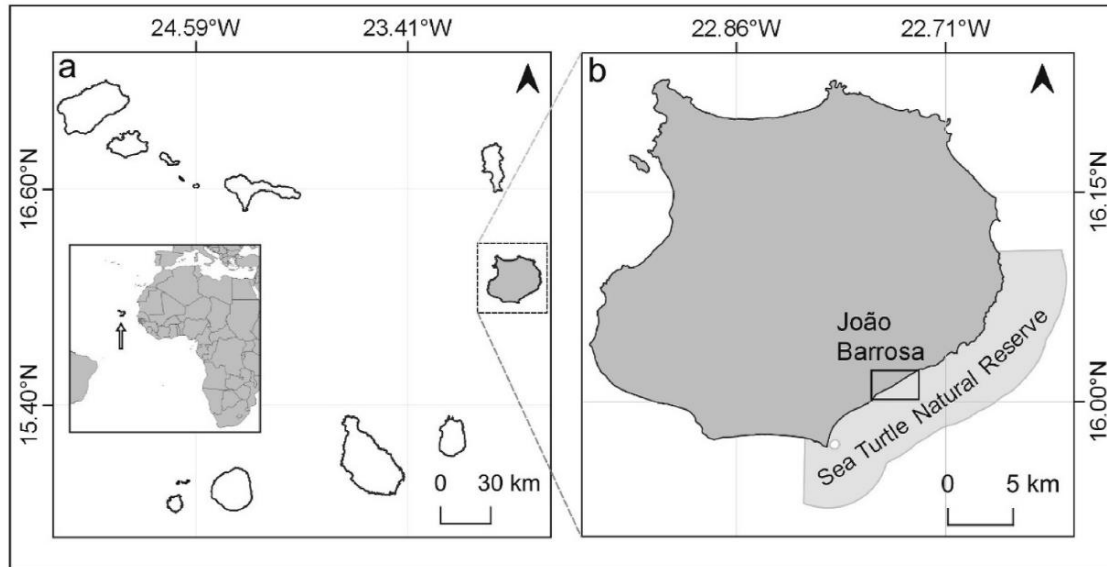
nesting turtles and nests deposited by turtles in arribadas (synchronized, mass nesting) showed a significant difference in predation rate. While 51 % of individually nesting turtle nests were preyed on, only 7.6 % of arribada nests faced predation within the first night (Eckrich and Owens, 1995).

This thesis aims to analyze the effect of nest abundance of Loggerhead turtles on the nest predation by ghost crabs on Boa Vista, Cabo Verde. The annual nest abundance on the studied beach is known to fluctuate greatly (Marco *et al.*, 2018), however it has been increasing overall during the period studied in the present work. The variability of recorded annual nest abundance combined with the results collected from monitored nests from each season is used to analyze the mean nest mortality and especially mean mortality caused by crabs correlated to nest abundance. These insights can help to improve the understanding of this predator-prey interaction and to advance conservation management and efforts for the endangered species *C. caretta*.

## **Material and Methods**

### **Study area**

This study was carried out on a North-East Atlantic Loggerhead subpopulation that nests in the Cabo Verde Archipelago. Cabo Verde is located in the eastern Atlantic, about 570 kilometers off of the western coast of Africa. Boa Vista, the most eastern island of the Archipelago, hosts around 60% of the Loggerhead nests in Cabo Verde (Marco *et al.* 2021). Data was collected on the 5km long nesting beach of João Barrosa, located on the southeastern coast of Boa Vista, for the nesting seasons from 2013 to 2021 (Martins *et al.*, 2022). The nesting season for *C. caretta* in Cabo Verde takes place between May 15 and October 30, peaking between July 15 and October 15 (Marco *et al.*, 2012). The incubation period of the nests lasts from mid-June to the end of November as the incubation durations of each nest range from approximately 49 to 61 days (Rocha *et al.*, 2015). Therefore, the egg predation period also occurs from mid-June until the end of November. During the peak of the season, the beach is monitored daily from nightfall until morning. For the monitoring, the beach of João Barrosa is divided into two parts for the years 2013 to 2018 (Norte and Sul) and three parts (Norte, Sul, and Sul Final) for the years 2019 to 2021.



**Fig. 2.1** Maps of the Archipelago of Cabo Verde (a) and Boa Vista (b). The beach of João Barrosa is located in the Sea Turtle Natural Reserve on the southeastern coast of Boa Vista (Martins *et al.*, 2021).

### **Nest abundance**

The nest abundance is defined as the sum of nests found during the nesting process at night and nests found based on tracks at dawn. All nests found were circled and marked with an “X” and the location was recorded using a GPS receiver (Garmin eTrex®). Following the night patrol at dawn, the entire beach area was patrolled again, registering all unmarked tracks made by the females since the last survey. The tracks were classified into four categories: tracks with a nest, tracks without a nest, unclear tracks, and incomplete tracks. In 2020 and 2021, only tracks with a nest were registered due to high nesting numbers. To avoid double-counting, the tracks were marked by patrol members, using their feet or a stick to draw a wavy line along the tracks.

### **Monitoring Nest**

The data used to evaluate the predation of ghost crabs on *C. caretta* nests was collected by marking and monitoring natural nests. The number of monitored nests is similar for each section of the beach (Norte, Sul, and Sul Final). From the end of June to mid-September, within each section of the beach, usually, one additional nest was marked every other day for monitoring purposes, although the number of nests monitored per season differs strongly. Numbers range from 60 nests monitored in 2014 to 203 nests monitored in 2019. The nests were randomly chosen and therefore randomly distributed throughout the sections. Clutch sizes were counted during oviposition. The laying time and date for each nest were documented. Subsequently, the nests were marked with a stick buried into the sand and the location was recorded using a GPS



receiver (Garmin eTrex®). During the morning surveys, all marked nests were monitored daily from the first day of incubation until exhumation. All nests were checked for any evidence of predation, inundation, erosion, or any other relevant disturbances to the nest. The predation by ghost crabs was detected using the presence of circular holes close to the nests. After registering the number of crab holes, they were covered to avoid double counting the following day. The inundation of nests by high tide, flooding, or storms was registered based on the moisture level of the sand surface. Double counting was avoided by drawing a line parallel to the ocean in front of the nest. If the tide reached the nest again, it would have washed away the line. Furthermore, all marked nests were checked for signs of emergence, such as tracks of hatchlings that emerged from the nest or depression of the center of the nest. All marked nests were exhumated, usually either three days after indications of emergence or when the nest completed 60 days. Closed eggs (eggs that did not hatch) and hatched eggs were counted. The number of hatched eggs was determined by counting complete shells and putting partial shells together until they added up to one egg. The number of turtles that hatched and were still within the nest was also registered; a differentiation was made between alive and dead turtles. The same procedure was done for the turtles that were in the process of hatching during exhumation. The closed eggs were assigned to one of 9 visual embryonic stages as described by Miller (1985) and Abella, Marco and López-Jurado (2007). Eggs with no visible sign of an embryo were classified as stage 0. After exhumation, the remains were buried in the same hole of the nest imitating the natural dynamics of a nest.

### **Calculations**

The relative hatching success of each marked nest was estimated by dividing the number of eggshells by the initial clutch size counted during oviposition, followed by a multiplication of the quotient by 100%. The nest mortality was calculated as the difference between 100% and the survival of the nest. The survival of the nest was calculated as a percentage as the sum of the number of shells and live-pipped turtles divided by the initial clutch size and multiplied by 100%. The nest mortality due to crab predation in percent was calculated by dividing the initial clutch size minus the number of eggshells, the number of enclosed eggs, the number of live-pipped turtles, and dead-pipped turtles (dead turtle that is half in, half out of its eggshell) by the initial clutch size and multiplying the quotient by 100%.

The percentages of predated and fully predated nests relative to the total number of monitored nests were calculated. Predated nests are nests attacked by crabs at least once during the incubation period. Fully predated nests refer to nests where no eggs were found in the egg chamber and intense predation during the incubation period was observed.

### **Data processing**

Monitored nests excluded from the data analysis (besides for analysis of mean clutch size) were nests where the stick marking the nest was taken by turtles or lost for no apparent reason. Monitored nests with a second nest in the same spot were also excluded for data analysis (besides for analysis of mean clutch size). Exhumed nests with no eggs or shells found were considered as entirely predated or swept away by the sea and assigned mortality of 100% as well as nests that were lost or removed due to extreme predation or inundation. Nests that were lost or had to be removed due to intense predation were categorized as fully predated nests. Nests, where the eggs were taken by the sea, were set to 0% mortality by crab predation as the eggs were swept away rather than predated. Nests that were not found and the missing eggs could not be assigned to inundation or predation due to missing observations during monitoring were excluded from the analysis of the mortality by crab predation.

The method of egg and eggshell counting to study nest mortality harbors errors. These manifest themselves in over- or underestimation of hatched eggs when putting partial shells together until they added up to one egg and errors in counting. The method of counting hatched eggs based on eggshells is estimated to have an accuracy between 92 and 100% (Fowler, 1979). However, lower accuracy was observed during this data collection. Furthermore, mistakes in counting during oviposition or during exhumation and overestimation of hatched eggs can cause negative mortality values if the number of total eggs counted during exhumation exceeds those counted during oviposition. The egg error (difference in the number of eggs counted at oviposition compared to exhumation) is positive when the hatched eggs are underestimated due to either false counting or eggs being taken by crabs or the sea during the incubation period. Additional variance exists as the data for this study was collected by numerous people. The data was not cleaned any further apart from the cases described above. The errors caused by the method cannot be fully removed. Therefore, no cleaning of the data was done to not create data bias. The method was used despite the variance and errors presenting themselves as it allows

for the collection of a high amount of data in a study area that is remote with limited possibilities.

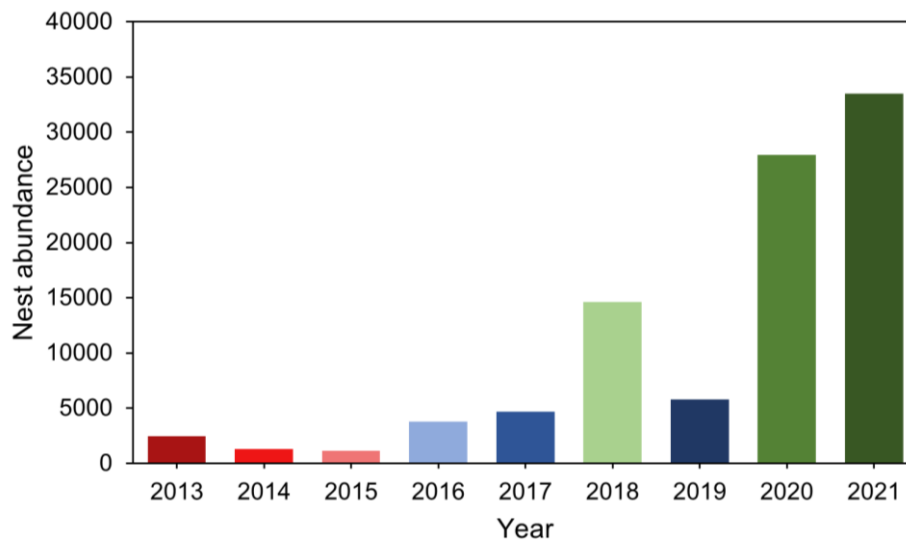
### **Data analysis**

The statistical analysis was carried out using the software R i386 4.0.5. The Shapiro-Wilk-test was used to evaluate the normality of the data. It showed that the data for nest mortality and nest mortality due to crab predation were not normally distributed. The Bartlett-test was used to test the homogeneity of variances. It showed heterogeneity for both variables. Due to the absence of normal distribution and homogeneity of variance, a non-parametric analysis was done. The nest mortalities of the different nesting seasons were compared to each other through pairwise comparisons using the Wilcoxon rank sum test with the continuity correction "Bonferroni" at a 0.05 confidence level ( $\alpha$ ). The same procedure was done to analyze the mortality by crab predation. The mean nest mortality of each season was used in analyzing the correlation between nest mortality and nest abundance. Because the nest abundance did not show normal distribution, the Spearman correlation was used to examine the correlation. The same procedure was done to analyze the correlations between mean hatching success and nest abundance, between the mean number of crab holes and nest abundance, between mean days predated to nest abundance, and between mean nest mortality by crab predation and nest abundance. Due to the monotony of the data, the correlation between the mortality by crab predation and the number of crab holes and the correlation between mortality by crab predation and the number of predated days was analyzed using the Spearman correlation.

## **Results**

### **Nest abundance**

The nest abundance on João Barrosa for the studied period from 2013 to 2021 was highly variable as shown in Figure 2.2. The seasons at the beginning of the study period (2013, 2014, and 2015) showed low nest abundance (2472, 1306, and 1123 nests) with 2015 having the lowest recorded nest abundance. After the season 2015, the nest abundance increased annually until 2018 (3778, 4688, and 14595 nests). In 2019, the recorded nest abundance was 5794 nests. The highest nest abundances were recorded in 2021 (33496 nests) and 2020 (27955 nests).

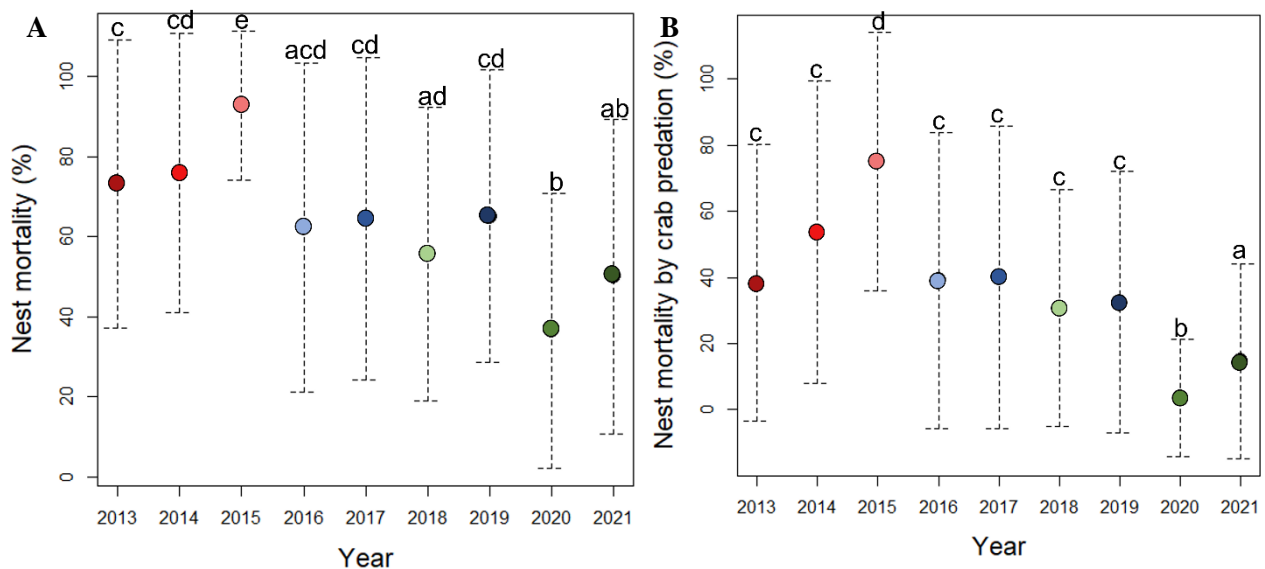


**Fig. 2.2** Nest abundance on João Barrosa, Cabo Verde in the years 2013 to 2021. Each bar shows the total number of nests recorded for the seasons between 2013 to 2021. Green color indicates the three seasons with the highest nest abundance, red indicates the three seasons with the lowest nest abundance and blue indicates the three seasons with the nest abundance in middle. The shades within the three colors get lighter with lower nest abundance.

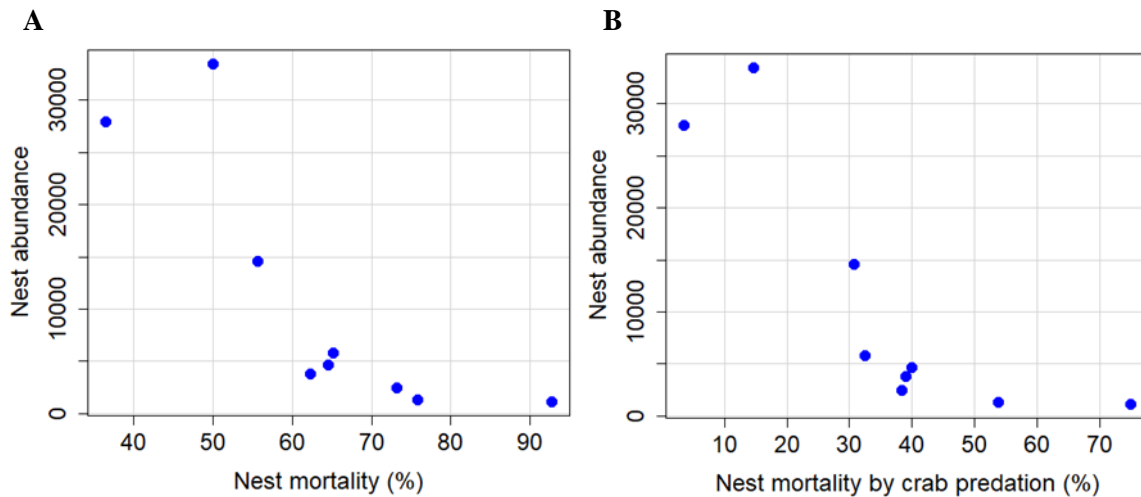
### Monitoring Nests

The mean nest mortality and nest mortality by ghost crab predation for the seasons 2013 to 2021 are shown in Figure 2.3. The mean nest mortalities ranged from 36.49% to 92.77%. The highest nest mortality with 92.77% (SD  $\pm$ 18.59, N=111) was recorded in 2015 and was significantly different from those of the other nesting seasons (Wilcoxon rank sum test, pairwise comparison,  $p$ -values  $< 2e-16 - 0.002$ ). The lowest nest mortality with 36.49% (SD  $\pm$ 34.35, N=95) was recorded in 2020. The nest mortality from 2020 was significantly different from all other seasons ( $p$ -values  $< 2e-16 - 0.001$ ) besides 2021 ( $p$ -value=0.229), which was the season with the second lowest mortality (49.99%, SD  $\pm$  39.24, N=127). The years 2013 (73.17%, SD  $\pm$  36.14, N= 87), 2014 (75.88%, SD  $\pm$  34.94, N=60), 2016 (62.28%, SD  $\pm$  41.04, N=118), 2017 (64.49%, SD  $\pm$  40.35, N=157) and 2019 (65.13%, SD  $\pm$  36.62, N=198) were not significantly different to each other regarding the nest mortality ( $p$ -values=1). The nest mortality in 2018 was revealed to be the third lowest with 55.69% (SD  $\pm$ 36.75, N=117) and was significantly different to the seasons of 2013 ( $p$ -value=0.0409), 2015 ( $p$ -value=7.8e-14) and 2020 ( $p$ -value=0.001). The nest mortality showed a very strong negative correlation relative to the nest abundance ( $r_s = -0.917$ ,  $p$ -value=0.001, N=9) (Figure 2.4). The mean nest mortality by crab predation ranged from 3.53% to 75.01% in the years 2013-2021. In the years between 2013-2019 excluding 2015, the mean nest mortalities by crab predation ranged from 30.65% (SD

$\pm 35.82$ ,  $N=115$ ) to 53.73% ( $SD \pm 45.69$ ,  $N=60$ ) and were not significantly different from each other (Wilcoxon rank sum test, pairwise comparison  $p$ -values=0.230 - 1). The mean nest mortality by crab predation in the season of 2015 (75.01%,  $SD \pm 39.13$ ,  $N=109$ ) was the highest and significantly different from all other seasons (Wilcoxon rank sum test, pairwise comparison,  $p$ -values $<2e-16$  - 0.001). The lowest mean nest mortality by crab predation was recorded in 2020 (3.53%,  $SD \pm 17.73$ ,  $N=95$ ) and was significantly different from all other seasons (Wilcoxon rank sum test, pairwise comparison,  $p$ -values $< 2e-16$  -  $1.1e-05$ ). The mean nest mortality by crab predation in the season 2021 (14.59%,  $SD \pm 29.42$ ,  $N=127$ ) was the second lowest and significantly different from all other seasons (Wilcoxon rank sum test, pairwise comparison,  $p$ -values $<2e-16$  - 0.004). The nest mortality caused by crabs showed a significant strong negative correlation to the nest abundance ( $r_s=-0.917$ ,  $p$ -value=0.001,  $N=9$ ) (Figure 2.4).

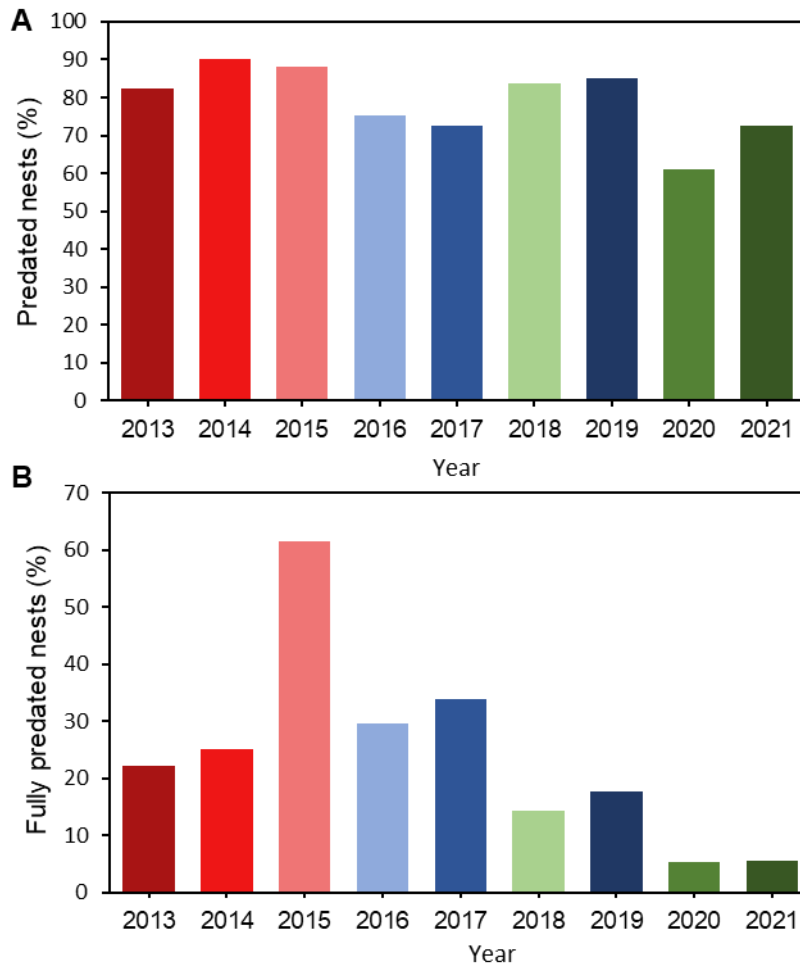


**Fig. 2.3** Mean nest mortality (A) and mean nest mortality caused by ghost crabs for the nesting seasons 2013 to 2021. The error bars represent the standard deviation (SD). Distinct letters represent significant differences between years as a result of the nonparametric Wilcoxon test with Bonferroni correction at the 0.05 confidence level ( $\alpha$ ). Green color indicates the three seasons with the highest nest abundance, red indicates the three seasons with the lowest nest abundance and blue indicates the three seasons with the nest abundance in middle. The shades within the three colors get lighter with lower nest abundance.



**Fig. 2.4** Correlation of mean nest mortality and nest abundance (A) and correlation of mean nest mortality caused by ghost crabs (B).

The percentage of the predated nest and fully predated nests by crabs are shown in Figure 2.5. During the season of 2013, 82.22% of the nests (N=90) were attacked by ghost crabs at least once during the incubation period, and 22.22% of nests (N=90) were fully predated by crabs leaving no eggs left in the nest. The following season, the percentage of predated nests increased to 90% (N=60), the highest value for the studied period, and the percentage of fully predated nests increased to 25% (N=60). In 2015, the relative number of predated nests decreased to 88.19% (N=113) and the relative number of fully predated nests peaked for the entire study at 61.47% (N=109). The percentage of predated nests in 2016 was 75.37% (N=121) and the percentage of fully predated nests was 29.57% (N=115). In 2017, the relative number of predated nests and fully predated nests increased to 72.62% (N=159) and 33.77% (N=151), respectively. Whilst the relative number of predated nests continued to increase in 2018 (83.89%, N=119), the relative number of fully predated nests decreased to 14.29% (N=119). In 2019, the percentage of predated nests was 85.19% (N=199); and 17.50% (N=198) of nests were fully predated. The lowest values of predated and fully predated nests were documented in 2020 with 61,22 % (N=95) and 5.26% (N=95), respectively. In 2021, 72.44% of the nests (N=126) were predated and 5.56% (N=126) were fully predated. The number of predated nests is strongly correlated to the number of nests ( $r_s=-0.717$ ,  $p\text{-value}=0.018$ ,  $N=9$ ) and the percentage of fully predated nests shows a very strong negative correlation to the number of nests ( $r_s=-0.833$ ,  $p\text{-value}=0.004$ ,  $N=9$ ).



**Fig.2.5** Percentage of predated (A) and fully predated nests (B) for the nesting seasons 2013 to 2021. Predated nests are nests that were attacked by ghost crabs at least once during the incubation period. Fully predated nests are those where no eggs were left in the nest chamber. Green color indicates the three seasons with the highest nest abundance, red indicates the three seasons with the lowest nest abundance and blue indicates the three seasons with the nest abundance in middle. The shades within the three colors get lighter with lower nest abundance.

Further results from the monitored nests in the study period are presented in Table 2.1. The mean clutch size varied between 78 and 88 and was strongly negatively correlated to the nest abundance ( $r_s=-0.683$ ,  $p\text{-value}=0.025$ ,  $N=9$ ). The hatching success ranged from 7.20% to 63.47%, peaking in 2020 and showing the lowest hatching success in 2015. The mean number of days predated during the incubation ranged from 2 to 6 days and showed a non-significant moderated negative correlation to the number of nests ( $r_s=-0.450$ ,  $p\text{-value}=0.115$ ,  $N=9$ ). The mean number of crab holes ranged from 6 to 25 holes and shows a significant strong negative correlation with nest abundance ( $r_s=-0.767$ ,  $p\text{-value}=0.011$ ,  $N=9$ ). Furthermore, the number of total days predated showed a moderate correlation ( $r_s=0.542$ ,  $p\text{-value}< 2.2e-16$ ,  $N=1000$ ) and

the number of crab holes showed a strong correlation to the nest mortality by crab predation ( $r_s=0.638$ ,  $p\text{-value}< 2.2e-16$ ,  $N=1000$ ).

**Table 2.1** Results of monitored nests regarding crab predation during the seasons 2013 to 2021. The standard deviation is shown in parentheses. Spearman correlation ( $r_s$ ) between the number of nests and mean clutch size, the mean number of days predated, and the mean number of crab holes and its p-value is shown.

Year	2013	2014	2015	2016	2017	2018	2019	2020	2021	$r_s$	p-value
Number of nests	2472	1306	1123	3778	4688	14595	5794	27955	33496		
Number of monitored nests	91	60	140	134	170	155	203	102	133		
Mean clutch size	86.30 ( $\pm 14.97$ )	80.45 ( $\pm 18.54$ )	88.04 ( $\pm 16.54$ )	81.50 ( $\pm 15.73$ )	80.33 ( $\pm 15.09$ )	85.76 ( $\pm 16.02$ )	77.77 ( $\pm 14.09$ )	79.18 ( $\pm 15.11$ )	78.03 ( $\pm 13.74$ )	-0.683	0.025
N for mean clutch size	88	60	139	129	166	153	203	102	133		
Hatching success (%)	27.14 ( $\pm 36.23$ )	24.12 ( $\pm 34.94$ )	7.20 ( $\pm 18.58$ )	37.58 ( $\pm 40.97$ )	35.49 ( $\pm 40.03$ )	44.27 ( $\pm 36.74$ )	34.80 ( $\pm 36.56$ )	63.47 ( $\pm 34.39$ )	51.15 ( $\pm 38.90$ )	0.917	0.001
N for hatching success	86	60	11	118	155	227	198	95	124		
Mean number of days predated	3.64 ( $\pm 3.17$ )	5.14 ( $\pm 3.78$ )	4.53 ( $\pm 3.41$ )	2.90 ( $\pm 2.94$ )	2.80 ( $\pm 2.84$ )	3.01 ( $\pm 3.27$ )	5.66 ( $\pm 5.37$ )	2.15 ( $\pm 2.80$ )	3.61 ( $\pm 3.98$ )	-0.450	0.115
Mean number of crab holes	14.59 ( $\pm 20.77$ )	24.78 ( $\pm 26.27$ )	24.43 ( $\pm 22.57$ )	10.90 ( $\pm 17.16$ )	8.91 ( $\pm 14.84$ )	8.28 ( $\pm 13.38$ )	18.13 ( $\pm 27.94$ )	6.01 ( $\pm 16.40$ )	10.69 ( $\pm 19.29$ )	-0.767	0.011
N for predated days & crab holes	85	58	99	107	152	114	189	95	117		

## Discussion

The outcome of this study provides insights into the effect of nest abundance of Loggerheads on nest predation by ghost crabs by evaluating annual variability in nest abundance and monitoring select nests over nine years. The results are an important contribution to conservation as information on this predator-prey interaction regarding sea turtle abundance is scarce. The nest mortality by crab predation shows a strong negative correlation to nest abundance. The year with the lowest nest abundance had the highest nest mortality, reaching a maximum value of 75%. In contrast, the nest mortality by crab predation is reduced to 4 to 15% in years with high nest abundance. The risk of a nest being predated as well as the risk of it being fully predated decrease with increasing nest abundance.

Higher Loggerhead nest abundance reduces predation risk by ghost crabs as well as the extent of predation. With higher nest abundance, the capacity of the ghost crab population on the studied beach to consume sea turtle eggs may be exceeded, therefore fewer nests are predated or fully predated. The satiation of a sea turtle egg predator has been observed before by Eckrich and Owens (1995). Their findings showed that the nests of Olive Ridley turtles which nested



solitarily faced significantly higher predation rates during the first night after oviposition compared to nests deposited in arribadas. The satiation of predators due to high prey abundance has been observed in numerous predator-prey interactions including birds preying upon insects and insects preying on seeds (O'Dowd and Gill, 1984; Williams, Smith and Stephen, 1993).

The higher nest mortality by crab predation in seasons with lower nest abundance may also be explained by a study investigating attack probability and the relationship between prey density and prey encounter rate in three-spined sticklebacks. The probability of prey first encountered being attacked increases as prey density decreases. Furthermore, experiments have shown an increasing encounter rate with increasing prey density like assumed in classical theory; however, the observed increase was slower than linear (Mols *et al.*, 2004; Ioannou, Ruxton and Krause, 2008). The combination of these two observations may explain lower total predation rates for seasons with higher nest abundance.

Ghost crabs preying on up to 75% of sea turtle eggs shows the huge impact they can have on overall hatchling production, specifically in years with lower nest abundance. Conversely, studies have reported little effects of ghost crabs in egg loss and described crabs as scavengers rather than predators (Stancyk, 1995; Bouchard and Bjorndal, 2000; Madden *et al.*, 2008). High predation rates on sea turtle eggs have also been observed on Cousine Island, Seychelles, a small oceanic island like Boa Vista. Compared to João Barrosa, the nesting beach is smaller (900 m in length) and has a lower abundance of 70 to 130 nests each season. In some years, predation rates of up to 90 or even 100% in preferred nesting zones have been observed (Hitchins, Bourquin and Hitchins, 2004; Gane *et al.*, 2020). Similar to the studied site on Boa Vista, ghost crabs are the only observed predators of eggs on Cousine Island and thereby causing high predation rates each year.

The absence of predators of ghost crabs and good beach quality may lead to high crab density, explaining the extremely high predation rates at lower nest abundance. The presence of large predators of sea turtle eggs on nesting beaches has been shown to reduce crab predation (Barton and Roth, 2008). As there are no predators besides humans who occasionally use big crabs as bait, the density of crabs is not limited by any predator. Additionally, ghost crabs are considered great bio-indicators of beach quality as they are sensitive to anthropogenic factors (Schlacher *et al.* 2011). Urbanization of beaches can reduce the population density of crabs (Noriega, Schlacher and Smeuninx, 2012; Barboza *et al.*, 2021). Vehicle traffic on sandy beaches and

tourism can further impact ghost crabs negatively by increasing the mortality rates (Hobbs III, Landry and Perry III, 2008; Schlacher, de Jager and Nielsen, 2011; Costa and Zalmon, 2019; Costa *et al.*, 2020). On the contrary, João Barrosa is a remote beach with no urbanization taking place and controlled sea turtle-watching tourism (Marco *et al.*, 2021). Low human impact and the lack of crab predators may lead to a big stable population of ghost crabs on Boa Vista. The spatial distribution pattern, intensity of predation, and thermal factors affecting ghost crabs have been studied on Cabo Verde; however, information about density in different years is lacking as well as information regarding the time period outside the nesting season of Loggerheads (Marco *et al.*, 2015; Rodrigues *et al.*, 2016; R. Martins *et al.*, 2022).

The number of crab holes observed during the incubation period showed a positive correlation to nest mortality by crab predation ( $r_s=0.638$ ,  $p\text{-value}< 2.2e-16$ ,  $N=1000$ ). The size of the crab holes was not recorded. A study investigating the pattern and intensity of ghost crab predation in Cabo Verde observed that small and medium size ghost crabs very often preyed on sea turtle nests. Nests preyed on by larger crabs showed a lower predation rate which indicates that bigger individuals may control the entire nest and defend the nests against smaller crabs (Marco *et al.*, 2015). Investigating stable nitrogen isotope ratios from ghost crabs, Barton and Roth (2008) discovered that larger ghost crabs feed at a higher trophic level and may consume more turtle eggs. However, crab holes cannot be solely used to access the predation rate; it is necessary to also determine the clutch size during oviposition and exhume the nest after the incubation period to get valid results.

On Cabo Verde, sea turtle eggs are only a temporal food item for crabs as they are only seasonally available for around 4 consecutive months. Ghost crabs shift their diet based on prey and food availability; therefore, alternative food sources are consumed during the rest of the year (Gül and Griffen, 2020). However, feeding assays discovered that ghost crabs preferred animal flesh (Rae, Hyndes and Schlacher, 2019). Due to the ghost crab's omnivorous diet, its survival does not depend solely on the availability of turtle eggs and hatchlings (Marco *et al.*, 2015). Ghost crabs are opportunistic feeders which indicates that the interannual variability in nest abundance would have no significant effect on ghost crab abundance (Marco *et al.*, 2015; Gomes do Vale *et al.*, 2022). As this study was done in nine consecutive seasons, a possible effect of interannual variability in nest abundance on the ghost crab abundance should have been observed.

The annual nest abundance in Cabo Verde is highly variable during the study period ranging from 1123 nests in 2015 to 33496 nests in 2021. Interannual variability in nest abundance can be observed in all seven sea turtle species and may be explained by the variation in the number of years females pause from nesting (Hays, 2000). During nesting season, sea turtles nest numerous times but usually only breed every 2 to 5 years, rarely nesting in two consecutive seasons (Marco *et al.*, 2018). The interval between two nesting periods of an individual may be influenced by environmental factors such as feeding conditions. High food availability might reduce the interval between two nesting seasons explaining seasons with high nest abundance (Carr and Carr, 1970; Hays, 2000). Furthermore, it is suggested that the extent of interannual variability of nest abundance is reflecting the trophic position (Broderick, Godley and Hays, 2001). Among the sea turtle species, Loggerhead turtles belong to the species with the lowest interannual variability (Hays, Mazaris and Schofield, 2022). As Loggerheads feed at a relatively high trophic level and their prey consisting of bivalve mollusks and other benthic invertebrates are relatively stable in abundance across years, their interannual nest number variability is comparatively low (Bjorndal, 2017). However, the interannual variability in nest abundance observed in this study is relatively high. This might be explained by an increase in overall population size as the four highest nest abundances were recorded in the last 4 years of the study period. Additionally, the interannual variability in nest abundance may be a predator prevention strategy as higher nest numbers reduce predation risk. Cumulative egg survival over the years may be higher with interannual variability rather than equal nest abundance due to the seemingly dominant effect of high survival rates in years of higher nest abundance as opposed to low survival rates in periods of lower nest abundance.

The consequences of the predation rates for the subpopulation studied will only be visible in a few decades as the age of sexual maturity for Loggerheads varies greatly among individuals and is estimated to be between 10 and 39 years (Avens and Snover, 2013). The Northeast Atlantic subpopulation which mainly is nesting in Cabo Verde is categorized as Endangered on the IUCN Red List (Casale and Marco, 2015). Studies of populations as well as simulations indicate that survival in the early life stages such as egg survival is of relatively high importance to recovery for Loggerhead populations (Dutton *et al.*, 2005; Mazaris, Fiksen and Matsinos, 2005; Marcovaldi and Chaloupka, 2007). Mazaris *et al.* (2005) concluded that increased egg survival could stabilize population dynamics and even enhance population sizes by compensating for deaths in later life stages. This highlights the value of continued research and conservation work to reduce egg loss and increase hatching success.

Nest predation is a challenging task for the conservation of sea turtles. This research shows that high nest abundance reduces mortality by predation. The highest hatching success in this study was recorded in 2020 with a value of 63%. In this season, the mortality caused by crabs was only 4%, and the total nest mortality was 36%. The hatching success of nests translocated to the hatchery on the studied beach João Barrosa is between 70 and 85% (Martins *et al.*, 2021). The other causes for mortality such as inundation, clay accumulation in the sand, roots, and fungus infection have not been assessed in this study but also play an important role in conservation efforts. Regarding nest predation, the impact of the hatchery relative to the *in situ* nest abundance is especially present in seasons of low nest abundance, because the ratio of translocated nests compared to *in situ* nests is high. As the study shows, low nest abundance leads to high predation rates and lower hatching success rates. Conversely, the hatchery presents a stable high survival rate. These two opposite trends further enhance the importance of the hatchery with respect to the overall survival rate in that season. However, other conservation strategies should be discussed for seasons of high nest abundance as the predation rate during those events is low and the impact of translocated nests therefore is low. Conservation efforts should also focus on juvenile and adult sea turtles as several population models have shown that their survival is critical to ensure an increase in population size (Heppel *et al.*, 1996; Heppell, Crowder and Crouse, 1996; Omeyer *et al.*, 2021). The findings of this study underline the importance of conservation efforts, especially for areas and seasons with low nest abundance.

The methodological choices for this study were constrained by limited resources like limited power supply as the study area is remote. Due to missing observations during the incubation period of the monitored nests, the number of predated and fully predated nests could be even higher than recorded. The reliability of these data is affected by errors caused by the method of egg and eggshell counting and the variance due to a high number of data collectors. The errors caused by the method cannot be fully removed, therefore, no cleaning of the errors was done to not create data bias. Nonetheless, the results are valid despite the variance and errors presenting themselves as a high amount of data was collected within the study area, reducing the impact of individual errors on the totality of collected data.

In conclusion, this research provides a new insight into the relationship between Loggerheads and ghost crabs, indicating a negative correlation between nest abundance of Loggerheads and nest predation by ghost crabs. Furthermore, it emphasizes the impact of ghost crabs as predators

of Loggerhead eggs as they can cause nest mortality rates of up to 75%. The knowledge gained from this study should be implemented in conservation efforts to increase their impact on the recovery of endangered populations. However, further research is needed to establish whether the ghost crab population size is affected by the availability of sea turtle eggs.

## **Acknowledgement**

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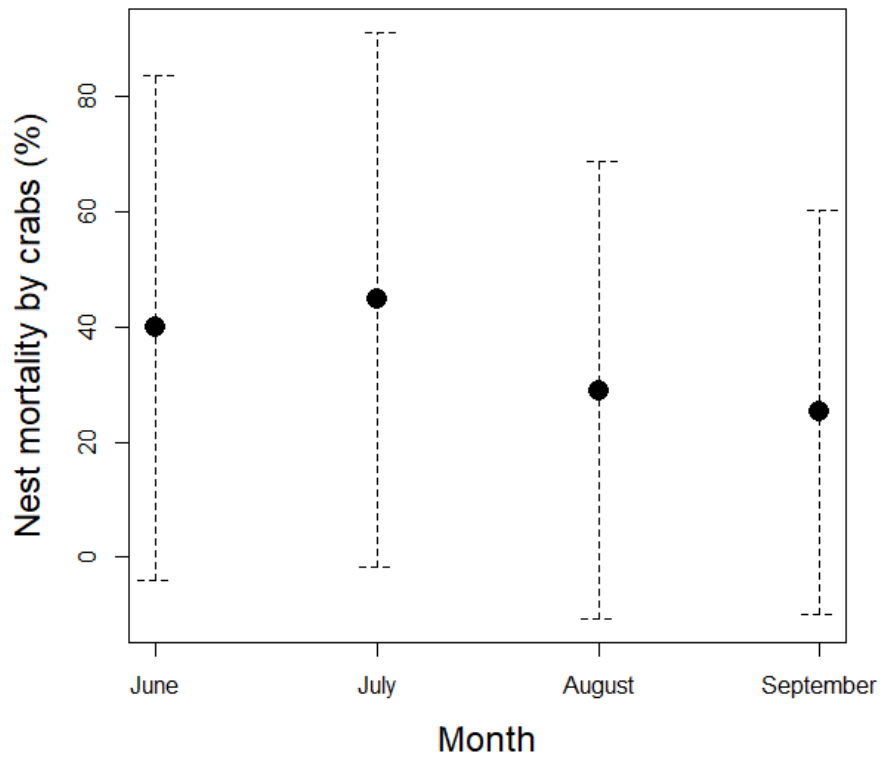
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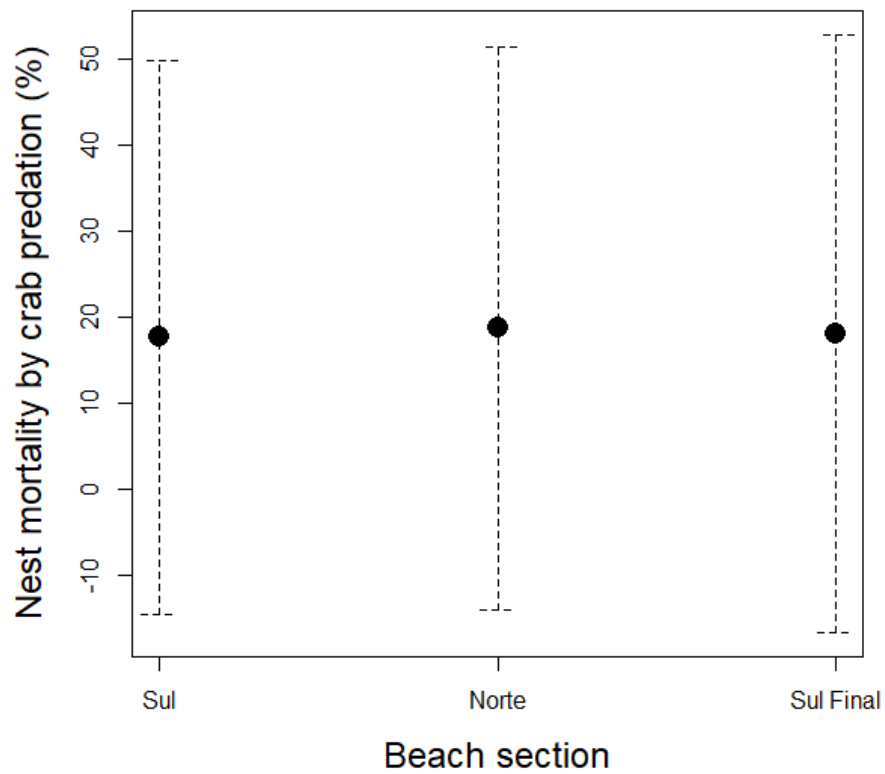
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**Appendix**



**Fig 2.6** Nest mortality by crab predation for the months June to September.



**Fig 2.7** Nest mortality by crab predation for the Beach section Sul, Norte and Sul Final in the years 2019 to 2021.