

Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population



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ABSTRACT

Predation is one of the most important threats to the early life stages of most endangered vertebrates. On small oceanic islands that host very important endangered sea turtle rookeries, ghost crabs are the main nest predators. Mortality in nests was evaluated on the island of Boa Vista which hosts around 75% of the nests in the Cape Verde archipelago, which is one of the world's largest loggerhead turtle (*Caretta caretta*) rookeries. In an extensive survey of the island, egg mortality significantly varied between beaches and averaged 70%. One of the main causes of egg mortality was predation by ghost crabs (*Ocypode cursor*) that stole an average of 33 eggs per nest. No other egg predator was observed during the study. In an intensive field experiment, the egg mortality for non-protected nests was 82% and ghost crabs predated an average of 50% of the total number of eggs. Even though female tracks on the beach are very conspicuous immediately after egg laying, very few nests were predated during this period. In contrast, most of the nests were predated at the end of the incubation period (after day 40 of incubation), when female tracks are not visible on the beach. Nests predated by larger crabs suffered a lower predation rate, suggesting that these larger dominant crabs defend the nest they prey upon. On-beach nest relocation had no significant influence on reducing egg predation. Females preferred nesting on beaches with higher hatching success although predation was not a risk that they seemed able to assess.

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1. Introduction

Many sea turtle populations are facing extinction and one of their main natural threats is nest predation. Opportunistic predators can easily consume the majority of sea turtle eggs every nesting season (Barton and Roth, 2008; Leighton et al., 2010). Sea turtles are known for coming to shore and laying their eggs on sandy beaches. Females dig nest chambers on the beach, and after oviposition they cover their eggs, camouflage the nest site and return to the ocean. During incubation, eggs are exposed to several threats that can cause a significant embryo mortality (Ditmer and Stapleton, 2012) such as beach flooding or erosion (Van Houtan and Bass, 2007; Wood et al., 2000), infections produced by microorganisms (Phillott and Parmenter, 2001; Sarmiento-Ramírez et al., 2010), poaching (Frazier, 1980; Hope, 2002), natural predation (Dodd, 1988; Donlan et al., 2004; Fowler, 1979) and even expected redundant impacts by off-road vehicles (ORVs) on sandy beaches (Schlacher et al., 2008). Carnivore mammals are considered the most important turtle nest predators (Ratnaswamy and Warren, 1998), and the regulation of

mammalian carnivores (e.g. raccoon *Procyon lotor* in Florida, USA) to reduce nest predation is a common practice (Barton and Roth, 2007; Pennisi, 2006). However, these mammalian carnivores also predate on ghost crabs (Mendonça et al., 2010) which are considered the second most important nest predator on many nesting beaches (Le Buff, 1990; Thompson, 1995; Trocini et al., 2009; Witherington, 1999). The reduction or absence of carnivore mammals seems to cause a significant increase in ghost crab abundance which leads to an overall increase on turtle nest predation (Barton and Roth, 2008; Brown, 2009; Pennisi, 2006).

Ghost crabs (*Ocypode* spp.) are the largest and most conspicuous invertebrates found in all tropical and semitropical 'ocean-exposed' sandy beaches around the world. Functionally they are the main bioturbators of beaches and form a key ecological link in the food webs of these ecosystems (Lucrezi and Schlacher, 2014). They have a planktonic larval stage that at a very small size transforms into a terrestrial animal that will live the rest of its life on the beach (Diaz and Costlow, 1972). *Ocypode* crabs are the fastest crustaceans on land and have acute senses of sight, smell, and hearing (Lucrezi and Schlacher, 2014). They dig deep, complex and sometimes voluminous sand burrows in the intertidal zone of closed beach areas where they remain during the warmer hours of the day, and show a crepuscular and nocturnal activity (Schuchman and Warburg, 1978). The main reason for this terrestrial

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behavior is their need to maintaining a high level of humidity on their gills so that they can breathe (Warburg and Shuchman, 1979; Weinstein et al., 1994). At night larger crabs can explore drier beach areas but smaller individuals are obliged to remain closer to the water. They are very sensitive to the trampling and compaction of the sand by humans and are considered a good bio-indicator of beach quality use (Lucrezi and Schlacher, 2010; Schlacher et al., 2011).

Several ghost crab species with a very wide geographical distribution, and with similar morphology and ecology, have been identified. They display extraordinary trophic plasticity, occupying several trophic role levels (e.g. scavengers), obtaining food through a variety of strategies, and consuming a wide diversity of prey (Lucrezi and Schlacher, 2014). Even though several studies are based on the predation of ghost crabs on turtle nests, overall there is little information about the pattern and behavior of these decapods when predated the nests. Lucrezi and Schlacher (2014) summarized ghost crab predation rates on sea turtle nests, eggs, and hatchlings (*Ocypode* spp.), although the compiled data is mostly focused on *Ocypode quadrata*, a species from the USA and French Guiana.

Ocypode cursor Linnaeus, 1758 has been found predated turtle nests on the western African coast and the Eastern Mediterranean (Aheto et al., 2011; Smith et al., 1996; Strachan et al., 1999). Former studies on the dispersal, population structure and burrow shape of *O. cursor* in northern Israel were conducted by Schuchman and Warburg (1978). Recently, a preliminar investigation was conducted on the species on the volcanic islands of Cape Verde (tropical Eastern Atlantic, Fig. 1) focused on population density and the spatial distribution of burrows (Rodrigues, 2012), and/or essays on the turtle nest detection behavior that those crabs presented (Frederico, 2013). This species is very abundant and predated loggerhead turtle (*Caretta caretta*) nests in Cape Verde, where no native or introduced carnivore mammal species is present. The island of Boa Vista (archipelago of Cape Verde) hosts the

biggest loggerhead rookery in the Eastern Atlantic (Marco et al., 2012), and ghost crabs are the only relevant predators of turtle nests there (Marco et al., 2011; Varo-Cruz et al., 2005). This rookery is reproductively isolated from the other Atlantic populations (Monzón-Argüello et al., 2010), having exclusive mitochondrial DNA haplotypes, which suggests that this isolation occurred a long time ago. The population has recently been considered the most endangered loggerhead population in the Atlantic and one of the most endangered sea turtle populations in the world (Wallace et al., 2011). Boa Vista, the easternmost and third largest island (620 km²) in the archipelago of Cape Verde, has volcanic products, minor intrusions and a thin partial sedimentary cover (Dyhr and Holm, 2010) where white sandy beaches are common and calculated to comprise around 46% of the total island coastline, estimated on 160 km (Almeida et al., 2012). The scarce human presence on many isolated beaches seems to be a prolific factor and has favored the existence of a high density of ghost crab populations (Barros, 2001).

The impact of ghost crab predation on nest survival has been assessed. To have knowledge on which areas, when, how and with what frequency ghost crabs attack nests and consume the eggs can provide an interesting insight into this singular predator–prey interaction, as well as provide relevant information to compile a risk assessment of this natural threat on endangered turtle populations. Additionally, the evaluation of management techniques to reduce this natural threat can help to improve the productivity of this population and reduce the risk of these sea turtles, catalogued as endangered, becoming extinct.

2. Materials and methods

Loggerhead turtle nest survival and ghost crab predation were studied during the 2005 season in the Reserva Natural da Tartaruga, the main nesting area on Boa Vista that hosts around 75% of the nests

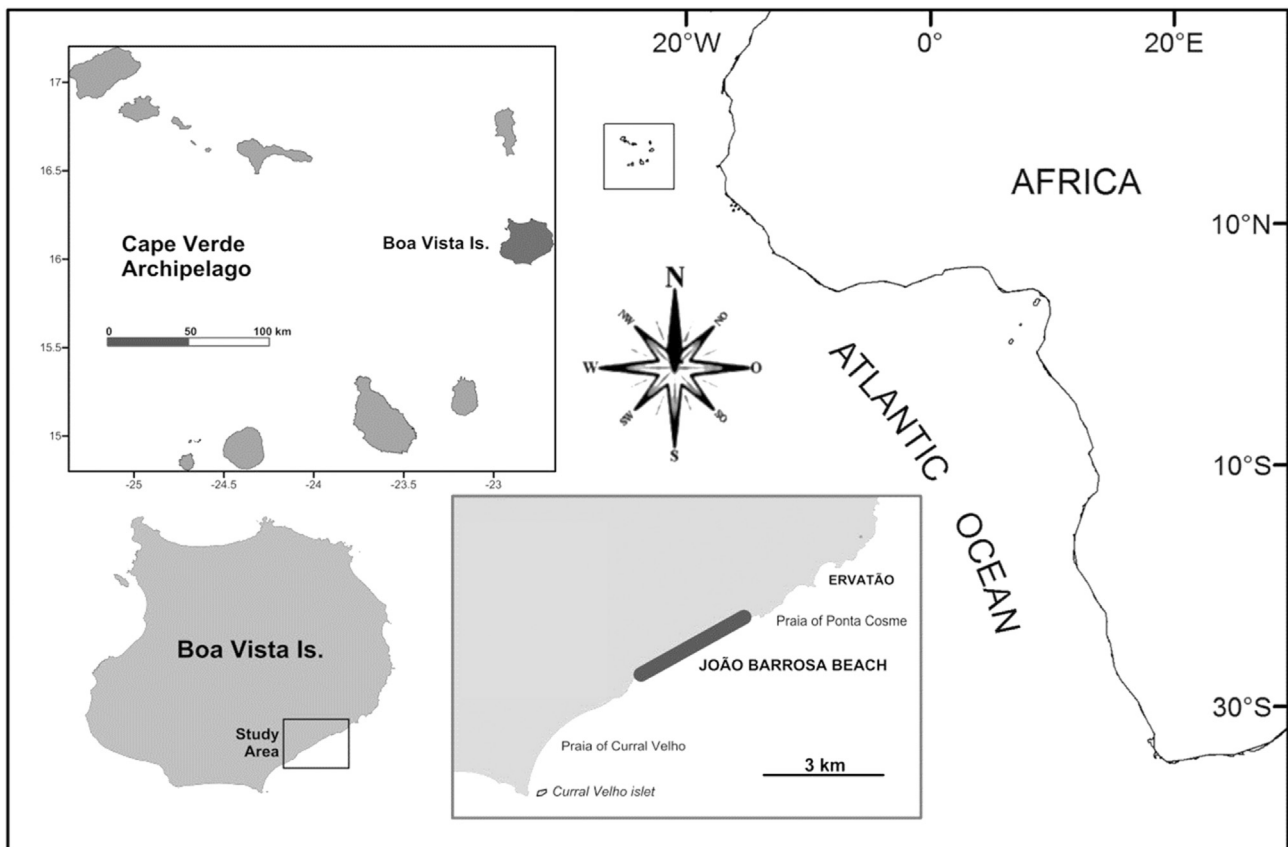


Fig. 1. Maps of Cape Verde, the island of Boa Vista and the study beach of João Barrosa in the southeast of the island.

laid on the island (Marco et al., 2012). This field study was conducted from Ponta Medronho (16.005° N, 22.760° W) to Ponta do Roque (16.085° N, 22.667° W) on the 6 beaches with the highest nest density: João Barrosa (2700 m), Barrosas (1200 m), Ponta Cosme (1800 m) and Ervatão (670 m), Calheta (375 m) and Lajedo Teixeira (150 m) (Fig. 2). All of these beaches are pristine, deserted, and without any significant

human influences. The dune area is reduced and features low halophytic shrubs. All females were PIT-tagged and identified and every nest corresponded to a different female. 215 nests (around 6% of the total number of nests laid in the area during that season) were selected in a stratified sampling that considered both the spatial and temporal variability on the 6 beaches (Table 1). Clutch sizes were directly counted

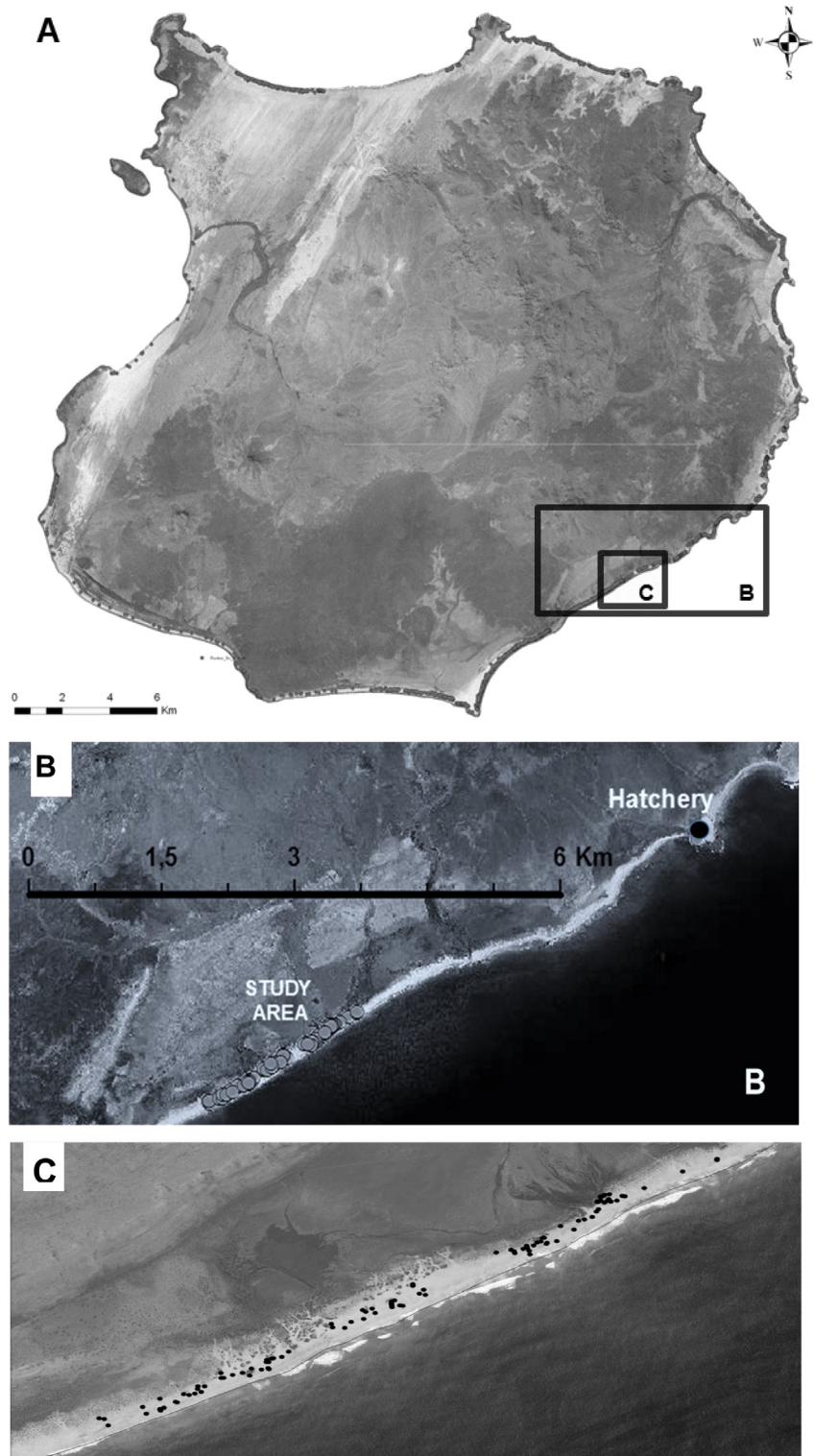


Fig. 2. A. Aerial photograph of Boa Vista Island showing the main nesting beaches and the distribution of loggerhead nests (dots) during the 2007 and 2008 nesting seasons. The large black rectangle indicates the coastal area of B. The small black rectangle (2) indicates the area of C. B. The area of the experimental study of 2008 and the hatchery (black dot) where some nests were relocated. C. Detail of the location of the nests (black dots) monitored during the field experiment in 2008. Orthophoto of Boa Vista – Cape Verde (40 cm per pix) 2010-UCCP MAHOT www.sit.gov.cv.

Table 1

Results of loggerhead nesting surveys and nest monitoring on 6 beaches of the island of Boa Vista (Cape Verde) during 2005. *Average values.

Beach	João Barrosa	Barrosas	Ponta Cosme	Ervatão	Calheta	Ladjedo Teixeira	Total
Beach length (m)	2700	1200	1800	670	375	150	6895
No. of nesting activities	4397	3507	6281	2817	2174	1532	20,708
Number of nests	1369	897	1411	619	713	440	5449
Nesting success (%)	31.1	25.6	22.5	22.0	32.8	28.7	26.3*
Number of monitored nests	38	21	45	38	45	26	213
Mean clutch size	82	86.1	84.3	85.7	82.2	80.4	83.4*
Hatching success (%)	50.2	26.6	16.3	34.8	54.7	47.4	39.0*
Estimated number of dead eggs	55,904	56,688	99,559	34,587	26,550	18,608	277,212
Egg mortality caused by crabs (%)	36.7	30.8	24.2	26.6	31.5	17.5	27.8

during oviposition or within the first 12 h of incubation. All nests were marked with a stick on the beach and the location was recorded using a GPS receiver (Garmin eTrex®). From the first day of incubation until hatchling emergence, all nests were monitored daily and any evidence of inundation, erosion, predation or any other relevant incidences over the nests were recorded. After day 45 of incubation, the emergence of hatchlings from the nests was recorded daily. From 5 to 10 days after the last massive emergence, the nests were exhumed. Nests where emergence was not observed after 70 days of incubation were exhumed. Additionally, 130 seemingly doomed nests (very close to the water or in flooding areas) were relocated to a beach hatchery immediately after egg-laying. The translocation procedure was identical for all nests. The eggs were obtained wearing latex gloves immediately after they came out from the cloaca. Eggs were transported to the hatchery (Fig. 2) on foot, isolating them inside sterile plastic bags, avoiding jerking or rotational movements. Clutches were reburied in the hatchery in standardized hand-dug cavities that resembled natural nests in shape, size, and sand characteristics (maximum nest depth = 50 cm). Two people performed the translocation operations. All experimental translocations lasted 30–70 min, depending on the distance from the original nest's location to the hatchery. During translocation, eggs spent ≤ 10 min in direct contact with air. A round plastic net (diam: 45 cm, ht: 50 cm) was placed over all nests in the hatchery 45 days after egg-laying to retain hatchlings, and therefore have the opportunity to count and measure them after emergence. After day 45, all nests were checked daily during the night and at daybreak to record hatchling emergence.

Loggerhead nest survival and ghost crab predation were also studied on the island of Boa Vista during the 2007 and 2008 nesting seasons. 46 freshly laid nests were randomly selected from a total of 52 km of beach coastline on the island, excluding those beaches studied during 2005. The nests were marked early in the morning within the first 12 h after oviposition. The nests were carefully excavated and eggs were extracted, avoiding any vibration or turning of the eggs, or any exposure to sunlight, and carefully deposited over wet sand extracted from the nest chamber. All eggs were counted and immediately reburied in the same nest hole, simulating the behavior of females after egg laying. After 70 days of incubation, the nests were exhumed using the same methodology as in 2005.

During the exhumation of all nests (from 2005, 2007 and 2008), the materials found were classified into the following categories: shells from hatched eggs, dead and alive hatchlings and non-hatched eggs. All non-hatched eggs were dissected and were assigned to the consequent categories: pigmented embryo, non-pigmented embryos and eggs without apparent development.

Nesting success was calculated dividing the number of nests by the number of nesting activities. Hatching success was calculated dividing the sum of the number of shells belonging to hatched eggs and the number of hatched turtles from the nest during exhumation by the initial clutch size. Emergence success was calculated dividing the number of shells belonging to hatched eggs that were retrieved during exhumation

by the initial clutch size. The impossibility of evaluating a hypothetical predation of hatchlings in the nests could be causing an overestimation of emergence success.

To more accurately evaluate the nest predation rate and the behavior and patterns of ghost crab predation on loggerhead nests, a field experiment was conducted from July to October 2008 in João Barrosa beach on the island of Boa Vista (Republic of Cape Verde) according to methodology used by several authors (Miller, 1999; Varo-Cruz et al., 2005). Additionally, in the same experiment the effectiveness of various techniques designed to reduce the mortality caused by nest predation and to improve the productivity of threatened populations were evaluated. João Barrosa beach (16.01° N, –22.75° W) is located in the southeastern part of the island of Boa Vista. The study area was located in the eastern part of the beach on a stretch of about 1.2 km. The beach there has white sand and a gentle slope with moderate hazard areas that become flooded at high tide. The area has no visible anthropogenic impact.

From the 16th to 28th July and on this study beach, 100 nests with recently laid eggs were selected, marked, and all eggs were carefully extracted and counted. Each nest was randomly assigned in a block design to one of 5 different experimental treatments. Twenty nests were reburied in the same place and left unprotected (EX = exposed); 20 nests were reburied in their natural locations but fully protected from egg predation inside plastic mesh cages (PR = protected); 20 nests were reburied in the same place and partially protected below a horizontal 1 m² plastic mesh located at a depth of 10 cm from the beach surface (ME = mesh); 20 nests were relocated to a different area within the same beach but where there was a lower risk of flooding, far from the shore, and were left unprotected (RL = relocated); and 20 nests were relocated to a hatchery without the presence of crabs (HA = hatchery). All nests were monitored every morning until hatchling emergence and the date, number, and diameter of the holes dug by ghost crabs over the nests to predate the eggs were recorded on a daily basis. The diameter of the crab hole is highly correlated and allows to make good estimate of the crab size (Strachan et al., 1999; Tureli et al., 2009; Valero-Pacheco et al., 2007). After emergence, hatchling tracks from nests belonging to the EX and RL treatments were counted daily, and hatchlings from nests belonging to PR, ME and HA treatments were counted and released onto the beach. All of the hatchlings reached the water in a few minutes. The duration of incubation was estimated as the number of days between the egg laying and the first massive emergence. All nests were carefully exhumed 5 days after the last emergence and the number of hatched eggs from every nest (reconstructing their eggshells), the predated eggs inside the nests, and the remaining unhatched eggs were recorded. The number of stolen eggs was estimated by subtracting the sum of the number of hatched and unhatched eggs inside the nests from the initial number of eggs. To estimate hatching success the difference between the number of initial eggs and the sum of the number of unhatched and stolen eggs was calculated, and then this value was divided by the initial number of eggs.

The study on the predation behavior of ghost crabs on loggerhead nests and the impact of this predator on the reproduction and

abundance of loggerheads was conducted using data from the nests assigned to the treatments EX and RL, where nests were incubated on the beach with no physical protections against crab attacks. Parametric ANOVA and Student t-test were used for where the variances of the different groups were not significantly different. Tukey post-hoc tests were used for pairwise comparisons.

3. Results

3.1. Beach surveys from 2005, 2007 and 2008

20,708 nesting activities and 5449 nests were recorded during the 2005 nesting season on the six beaches that host more than 60% of loggerhead turtle nestings in Cape Verde (7.7 km), within the Reserva Natural das Tartarugas. Nesting success varied between different beaches from 22 to 33% (Table 1). The vast majority of the nests were attacked by ghost crabs on all beaches (Fig. 3) and many of them were temporarily inundated by high tides during incubation. Many eggs were consumed inside the nests and others were stolen and transported to the crab refuges. At the end of the incubation period, it was a very rare occurrence to find remains of predated eggs inside the nest and fully predated nests were found completely empty.

During 2005 a 17.2% of nests were fully predated by ghost crabs. Mean hatching success on the 6 beaches was 39% (SD = 35.9, N = 214) ranging from 16.3 to 54.6 (Fig. 3). If monitored nests where all of the eggs were stolen by ghost crabs are excluded from the estimation, the value of hatching success goes up to 57% (SD = 36.8, N = 177). On nest surveys for the rest of the island during 2007 and 2008, mean

hatching success was 34.5% (SD = 33.6, N = 46). 15.2% of nests were fully predated by ghost crabs. The estimate of hatching success excluding these fully predated nests (those with no remains of eggs when exhumated) was 49.7% (SD = 37.5, N = 39).

In the hatchery, where there was no predation by ghost crabs, at exhumation the mean estimated number of eggs was 5.8 eggs lower than clutch size (N = 130; SD = 2.39). That value was considered as an error in the estimation of the number of eggs that are present in the nest at exhumation. Using that correction, the mean number of eggs stolen by crabs from the nests in the different beaches is of 23.2 eggs (N = 208; SD = 1.89; Fig. 3), a 27.8% of the eggs in the clutch, showing no significant variability among beaches (post hoc Tukey test: $P > 0.2$ in all pairwise comparisons). On average, 45.6% of egg mortality could be attributed to ghost crab predation in the study area (40% of nests laid in Cape Verde).

There was a positive correlation between nesting success and hatching success (Pearson correlation: $r^2 = 0.755$; $r = 0.8697$; $P = 0.025$). Beaches that are rejected as nesting sites with a higher frequency by females have higher egg mortality. However, there was no significant correlation between nesting success and the number of eggs stolen from the nests (Pearson correlation: $r^2 = 0.094$; $r = 0.306$; $P = 0.555$).

3.2. Field experiment

The ghost crab (*O. cursor*) was the only predator found excavating the sand around 79 of 80 nests studied in the beach. None of the nests in the hatchery was attacked by crabs. Only 5 of 80 nests were attacked during the first 15 days of incubation. From day 15 of incubation up to day 35 the nests were scarcely predated. Most of the predation events were produced after day 35 of incubation and the first attack on all nests took place on average at day 40 of incubation.

For unprotected nests (EX and RL) an average of 11.8 ghost crabs (SD = 11.79; 1–63) dug holes from the surface and reached the eggs. An average of 43.5 eggs (SD = 31.9, 49.1%, 0–100%) were stolen by crabs and extracted from the nest during incubation. The percentage of stolen eggs in each nest was independent of the clutch size (Pearson product–moment correlation: $r = 0.038$, $F = 0.050$, $df = 1, 34$, $P = 0.825$). A strong negative correlation was found between the number of eggs stolen from the nests and the hatching success of these nests, which shows that egg predation is a very important component of the variance in hatching success (Pearson product–moment correlation: $r = -0.861$, $F = 97.13$, $df = 1, 34$, $P < 0.0001$, $r^2 = 0.741$). The unprotected nests' average clutch size and hatching success were of 88.3 eggs and 36.3% respectively (Table 2) when eggs were counted immediately after being laid. However, the same nests' average clutch size and hatching success, when clutch size was wrongly calculated after incubation as the number of unhatched eggs plus the number of complete eggshells belonging to hatched eggs, were of 44.7 eggs and 67.5% respectively. The average hatching success increased to 71.5% when nests that had no eggs at exhumation were excluded from the analysis, which led to the estimate being double the correct value for the population (Table 2). (See Table 3.)

The rate of egg predation was negatively correlated with the average diameter of the crab holes (Pearson product–moment correlation: $r = -0.438$, $F = 8074$, $df = 1, 34$, $P = 0.0075$, $R^2 = 0.192$). A similar negative correlation was found between the average diameter of the holes and the hatching success (Pearson product–moment correlation: $r = -0.353$, $F = 5122$, $df = 1, 34$, $P = 0.030$, $r^2 = 0.125$). The rate of eggs stolen was independent of the number of nest-predating crabs (Pearson product–moment correlation: $r = -0.153$, $F = 0.956$, $df = 1, 38$, $P = 0.345$). The nests predated by big crabs had a smaller number of holes apparently because these large crabs reduced the access of smaller crabs to these nests.

In those nests that were completely protected (PR), crabs dug holes around the mesh cage but could not take the eggs or kill them. However, in the partially protected nests (ME) the average number of stolen eggs

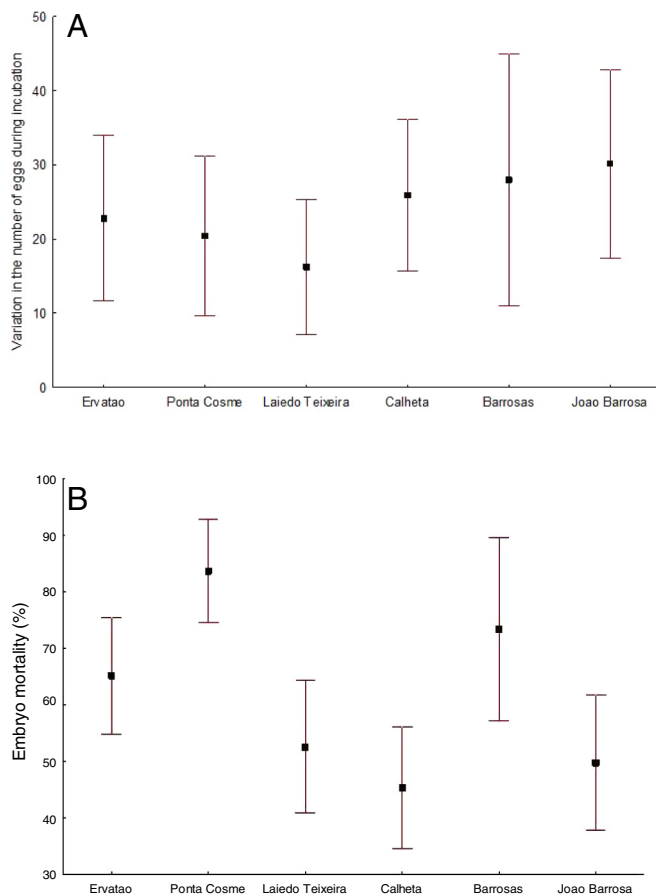


Fig. 3. A. Variation on the mean number of eggs from egg laying to exhumation into the nests located on 6 beaches with different levels of ghost crab predation and the beach hatchery without ghost crab predation. B. Mean embryonic mortality of the same nests located on 6 beaches with different levels of ghost crab predation and the beach hatchery without ghost crab predation.

Table 2

Average values of the main dependent variables recorded on nests exposed to the different experimental treatments. EX = fully exposed; PR = fully protected; ME = covered by a horizontal mesh; RL = relocated on the beach; HA = relocated in a beach hatchery.

Treatment	Incubation duration (d)	Clutch size	Hatching success	Stolen eggs by crabs (%)	Day of the 1st predation	Number of crab holes	Mean hole diameter (mm)
EX	55.8	87.2	32.5	54.5	39.4	14.8	72.6
ME	55.4	91.3	59.9	21.5	43.6	5.9	64.2
PR	55.9	85.9	82.2	4.4	36.5	10.9	65.9
RL	54.6	89.1	41.8	40.9	40.7	8.7	65.4
HA	59.2	90.8	64.6	2.1	–	–	–

by ghost crabs was of 20.3 eggs (SD = 29.9, 21.5%). This value was significantly lower than the one found in the EX nests ($t = 2.982$, $P = 0.0054$, $N = 36$) but larger than for PR nests ($t = 2.297$, $P = 0.033$, $N = 38$). Ghost crabs were able to detect and predate those nests protected by horizontal 1 m² meshes over the nests.

The average nest clutch size assigned to each treatment was similar (ANOVA test: $F = 0.378$; $df = 4, 95$; $P = 0.824$). However, hatching success for the different experimental treatments was significantly different (ANOVA, $F = 8.275$, $df = 4, 90$, $P < 0.0001$). The embryo mortality for unprotected and non-relocated nests was of 67.5% on average while on fully protected and non-relocated nests it was of 17.8% (Fig. 4). Ghost crabs directly predated or caused the collateral death of 50% of the eggs. The relocation of eggs to selected areas only decreased the mortality of non-relocated nests by less than 10% and the difference was not significant ($N = 36$, $t = 1.173$, $P = 0.249$) (Fig. 4). The relocation of eggs to a hatchery significantly reduced the mortality to 35.4% on average. The protection of eggs by placing a horizontal 1 m² mesh over the nest reduced the average mortality from 67.5 to 40%.

4. Discussion

Egg mortality is very high on Boa Vista beaches and ghost crab predation is one of the main causes of mortality. More than 98% of nests are attacked by crabs that can predate up to 50% of eggs on some important nesting beaches. A massive predation by ghost crabs is similarly observed on other islands in Cape Verde (A Marco pers. obs.). Other authors have found lower rates of loggerhead egg predation by click beetle *Lanelater sallei* (Coleoptera) larvae in Florida (USA) (Donlan et al., 2004). For instance, Caldwell (1959) found a 61% of loggerhead nests predated by crabs in South Carolina. The lack of large predators in Cape Verde and many other small oceanic islands may lead to a high crab density on beaches there. In Florida, where raccoons, click beetles and ghost crabs predate loggerhead eggs, the predation on turtle nests was highest where raccoon abundance was lower (Barton and Roth, 2008). However, the highest predation rate of raccoons and ghost crabs together was of a 31% of loggerhead nests.

Egg losses for other sea turtle species attributed to ghost crabs in small islands where bigger predators aren't present seem to be substantially smaller. For example, hawksbill turtle (*Eretmochelys imbricata*) nest predation by ghost crabs (*Ocypode cordimana*) on Cousine Island (Seychelles) was relatively low (approx. 17%) when there was

an absence of bigger predators (Hitchins et al., 2004) compared to the nest predation found in the present study. For green turtle (*Chelonia mydas*) nests, average predation by ghost crabs (*Ocypode ceratophthalmus* and *Ocypode kuhlii*) in the Malaysian island of Mak Kepit was also very low (approx. 1.3%) (Ali and Ibrahim, 2002). In Bissagos Islands (Guinea-Bissau), ghost crabs seem to predate only 1% of green turtle nests (Catty et al., 2002). Hawksbills and green turtles dig deeper nests where eggs are better protected from ghost crabs than those in the shallower loggerhead nests. Alternatively, there could be interspecific differences among ghost crabs in their predation rate upon turtle nests. Nest predation by *O. cursor* could be stronger than that from other ghost crab species.

In some locations, non-seasonal nesting or sequential nesting of different turtle species can almost continuously offer eggs to predators. However, the availability of eggs on many sea turtle nesting beaches is seasonal, lasting around 3–4 consecutive months. Therefore, for ghost crabs and other predators, turtle eggs are a temporal resource that they efficiently use, but alternative food sources are required for the rest of the year. Several studies show that when there is an absence in turtle eggs, ghost crabs may feed on many other species (Chartosia et al., 2010; Hitchins et al., 2004), which proves that their survival does not exclusively depend on sea turtle conservation. The ghost crab is an opportunistic feeder (Strachan et al., 1999; Trott, 1999) that feeds on particulate organic matter found in between the grains of sand, dead fish and other dead animals on the beach, as well as lizards, other crabs, insects, birds and small mammals (Hitchins et al., 2004). Due to the ghost crab's opportunistic trophic ecology, the inter-annual population fluctuations or the overall worldwide decline in sea turtle abundance would have no significant influence on ghost crab abundance.

Table 3

Bias of clutch size and hatching success of unprotected nests (EX-fully exposed and RL-relocated on the beach) estimating the clutch size during the exhumation (unhatched eggs plus eggshells of hatched eggs).

	N	Mean	SD	Min	Max
<i>Clutch size</i>					
CS at egg laying	36	88.28	15.51	48	126
CS at exhumation	36	44.75	30.73	0	103
<i>Hatching success</i>					
CS at egg laying	36	36.26	28.09	0	90.7
CS at exhumation	36	67.52	33.59	0	100

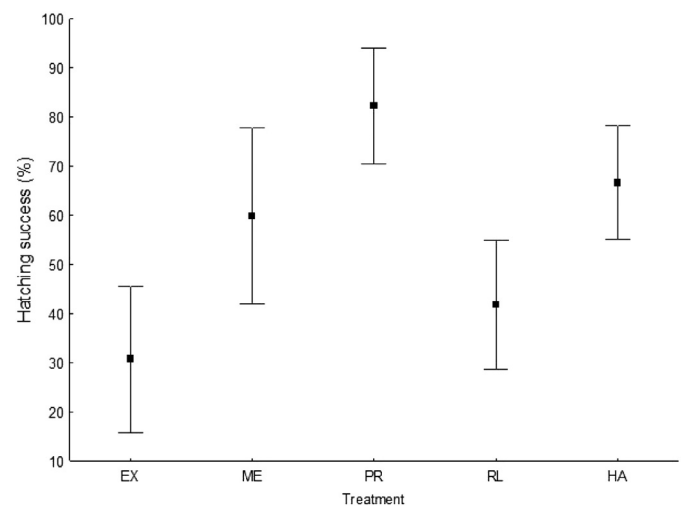


Fig. 4. Hatching success of loggerhead nests exposed to different incubation treatments. EX = fully exposed; PR = fully protected; ME = covered by a horizontal mesh; RL = relocated on the beach; HA = relocated in a beach hatchery.

Using stable nitrogen isotope ratios from ghost crabs, [Barton and Roth \(2008\)](#) found that bigger ghost crabs feed at a higher trophic level and may consume more loggerhead turtle eggs. Moreover, smaller crabs are more often found close to the sea, while bigger crabs are mostly found in places higher up the beach ([Strachan et al., 1999](#); [Tureli et al., 2009](#)) where turtles usually bury their egg masses. Thus, the bigger crabs could cause a deeper impact on loggerhead reproduction than the smaller ones. However, our data suggest that small and medium size crabs very often predate on turtle nests, and bigger ghost crabs may control entire nests and prevent the access to smaller crabs. This nest defense by bigger crabs may be a reason for smaller crabs to mainly feed at a lower trophic level (insects, small crustaceans). This intraspecific interaction may partially explain why the trophic segregation is due to a body size function ([Barton and Roth, 2008](#)). Stable ghost crab populations where big adults are relatively common may cause a lower predation risk for turtle nests. Traditional fishing methods in Cape Verde that consist of the use of large-sized ghost crabs as bait to catch big carnivore fish may increase the abundance of smaller crabs, and so increase predation rates on turtle nests. Some studies point out that ghost crabs are not common in the beaches' dry areas and that they are more common nearer to the sea ([Tureli et al., 2009](#); [Valero-Pacheco et al., 2007](#)). However, the present study shows that the nests relocated to drier areas near the dunes (TR) and far from the sea were intensively predated by crabs. The presence of nests on the beaches may be the cause for ghost crabs expanding their habitat to these drier areas.

Ghost crabs stole eggs from most of the nests and left no evidence of this interaction. In many cases, the number of stolen eggs was of great importance and sometimes the ghost crabs would completely empty the nest chambers leaving no remains of eggs or eggshells, or any nesting signals whatsoever. Thus, the estimation of clutch size and hatching success should be conducted with prudence. If researchers do not find any remains of eggs inside a supposed monitored nest and there are no external predation signals, they usually conclude that the nest had not been properly marked, monitored or identified, and that the nest chamber has been lost. In this event, the nest is usually excluded from the study. However, when ghost crabs are very abundant, the lack of eggs inside a monitored nest could be caused by a complete predation on it. In this event the predation rate would be 100% and the hatching success 0%. When the possibility of a full cryptic predation of a nest is relevant, precautions should be increased in the interpretation of a monitored nest that is not found. Hatching success and predation risk estimates can be significantly biased. Moreover, the lack of egg fragments in a predated nest is much more common when ghost crabs are present. In this case, clutch size can be significantly underestimated after the incubation. For example, the clutch size is necessary for calculating the embryo mortality and the hatching success, and eggs being stolen could bias the estimation of these two important demographic parameters. Because of this, on beaches with a relevant cryptic egg theft, the clutch size should always be counted at egg laying.

Predation risk was higher at the beginning of the incubation period and especially immediately after hatching. More than 80% of predation events were observed after day 45 of incubation. Another 15% of predation was observed in the first days after oviposition. Similar patterns of predation have been found in other turtle rookeries, sometimes even performed by very different predators ([Leighton et al., 2010](#)). [Frederico \(2013\)](#) experimentally tried to identify stimuli (e.g. chemical, thermal, mechanical and others) that ghost crabs use to identify turtles nests on the same beaches of the present study. The stimuli that predators use to find the eggs seem to be related with ecological or physiological processes that occur at the end of the incubation period. Apparently, female nesting behavior and specially the camouflage of the nest's location are very effective in reducing the risk of predation. These results reveal that the application of protective measures to reduce the impact of predation on nest survival should concentrate on the last week of incubation.

It is assumed that offspring fitness is the main factor influencing nest site selection ([Spencer, 2002](#); [Wilson, 1998](#)), especially when nest

survival is extremely low. It has been suggested that turtles might tend to lay at a certain distance from the water ([Hays et al., 1995](#); [Mortimer and Carr, 1987](#)). Furthermore, the success of digging attempts has been linked to sand characteristics ([Hays and Speakman, 1993](#)). However, there is low evidence of predation risk affecting nest site selection ([Spencer and Thompson, 2003](#)). In the present study nest survival significantly varied between different beaches and a clear relationship was found between nest survival and nesting success. However, nesting success was not apparently related to predation risk by ghost crabs. This indicates that other factors could be affecting female choice. For example, inundation causes a very important mortality on turtle nests ([Patino-Martinez et al., 2014](#)). In Boa Vista, many nests often become flooded on high density nesting beaches and all embryos die (A Marco pers. obs.). Females may be able to detect the level of sand surface moisture and thus choose to avoid wet areas. Alternatively, sex determination in sea turtles is mediated by incubation temperatures ([Bull and Vogt, 1979](#)) and females could choose certain nest sites to optimize hatchling sex ratio ([Janzen and Morgan, 2001](#)). Water content affects sand temperature and could therefore be a factor that influences the selection of warmer locations. Female turtles may also nest in dryer areas so as to lower the risk of flooding. With regard to nest predation, the lack of parental care in turtles could complicate the detection of nest predation risks, and be why this is not taken into account by nesting females.

Many loggerhead nesting populations (including Cape Verde) are threatened because of severe environmental impacts and illegal activities. In addition, sea turtles may be threatened by warming incubation temperatures, combined with temperature dependent sex determination, leading to severe hatchling sex ratio skews ([Laloë et al., 2014](#)). To preserve them, the enhancement of hatching success by reducing nest predation can be very important. The loggerhead rookery of Cape Verde is considered the second most important population in the Atlantic ([Marco et al., 2012](#)). This population shows significant genetic differences with all major Atlantic and Mediterranean loggerhead populations and is therefore reproductively isolated ([Monzón-Argüello et al., 2010](#)). For that reason, it has been considered a regional management unit ([Wallace et al., 2010](#)) that faces severe threats. A recent comparative analysis of the most important sea turtle populations around the world has showed that the Cape Verdean loggerheads can be considered the most endangered loggerhead RMU in the Atlantic, as well as one of the 11 most endangered sea turtle populations in the world ([Wallace et al., 2011](#)). Based on these study results, those nests located on beaches with high nest and crab density are going to experience a very high predation rate. A good management tool to increase survival when many nests are spatially concentrated is the relocation to a protected on-beach hatchery. On those islands and beaches that present a low nest density and a high crab abundance, a hatchery could be very inefficient and a better tool would probably be the direct protection of individual non-relocated nests on the beach. Physical protection, avoiding the use of metallic materials, would be especially useful at the beginning and at the end of the incubation period. The complete protection of nests from ghost crabs and other predators requires a significant amount of time and effort for each nest and it is only recommended when the number of nests is very scarce and these are far from each other. In these cases, the solitary nest protection can be very important at a population level, but the creation of special hatcheries for just a few nests is practically worthless. However, on beaches with a high nest abundance and predation risk, efforts to protect a relevant number of nests *in situ* are extremely costly. The creation of safe and protected hatcheries is highly recommended in these situations. The relocation of nests on the beach can be useful to protect nests from physical threats, but has been scarcely effective in preventing ghost crab predation.

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