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Ghost crab predation of loggerhead turtle eggs across thermal habitats

Rita Martins[a], Adolfo Marco[b], Juan Patino-Martinez[c], Kate Yeoman[c], Catarina Vinagre[d,e], Ana Rita Patrício[f,g,*,1]

[a] Centre for Environmental and Marine Studies, Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisbon, Portugal
[b] Department of Biodiversity Conservation and Ethology, Estación Biológica de Doñana, CSIC, Seville, Spain
[c] Maio Biodiversity Foundation (FMB), Maio Island, Cape Verde
[d] CCMAR, Centre of Marine Sciences, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal
[e] MARE, Marine and Environmental Sciences Centre, Faculty of Sciences, University of Lisbon, Campo Grande, Lisbon 1749-016, Portugal
[f] MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, 1140-041 Lisbon, Portugal
[g] Centre for Ecology and Conservation, Biosciences Department, University of Exeter, Penryn, Cornwall, TR10 9FE England, United Kingdom

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ABSTRACT

The reproductive success of sea turtles is highly influenced by the environmental and biological conditions of the nesting beach. Maio Island, Cabo Verde, one of the main nesting sites for the Northeast Atlantic loggerhead subpopulation, displays marked heterogeneity of sand coloration, with dark, mixed and light sandy beaches, resulting in different thermal habitats**.** Considering that sand temperature can influence both sea turtle embryo development and predatory activity by ghost crabs – the main predators of clutches and hatchlings at Cabo Verde – we surveyed loggerhead nesting beaches at Maio Island, with three sand colorations ('beach type'), to assess: 1) the density and size of ghost crab burrows, as a proxy for ghost crab density and size, and 2) ghost crab predation on 70 loggerhead nests. We further assessed nest site selection, by considering the number of nesting activities and clutches laid across beach type. There were no evident trends in the distributions of ghost crab density and size between years or beach type. We found that ghost crab predation is a major source of mortality in Maio Island, affecting 67.8% ($n = 59$) of the nests. Ghost crab predation was variable between beaches, but generally, at the warmer dark sand beaches, clutch mortality was mostly caused by ghost crab predation (53.2%, $n = 17$), while at the mixed sand beaches mortality by predation was low (7.5%, $n = 18$), compared to mortality due to other causes (49.9%), indicating that other factors can also significantly impact clutch survival. The mixed sand beaches had more nesting activities and higher nest density (2.29/m^2; 1.25/m^2, respectively), compared to the light sand (0.72/m^2; 0.35/m^2) and the dark sand beaches (0.73/m^2; 0.27/m^2), suggesting a possible predation-free nesting preference. Our findings show that some beaches are in need of nest protection, thus we recommend both in situ nest protection and egg translocation to safe hatcheries, depending on the threats identified, to enhance clutch survival at such heterogeneous nesting areas as Maio Island.

1. Introduction

Among egg-laying species with no parental care the nest location can be critical for clutch survival, since the surrounding conditions can determine important factors such as incubation temperature, vulnerability to flooding events and predation (Mortimer, 1990; Ackerman, 1997; Spencer, 2002; Marchand and Litvaitis, 2004; Kamel and Mrosovsky, 2005; Pike et al., 2015; Mansouri et al., 2020). Sea turtles are an excellent example of a group of species displaying no parental care, and that have the fate of their offspring intrinsically linked to the nesting site (Blamires et al., 2003; Kamel and Mrosovsky, 2005; Patrício et al., 2019). They are long-lived and late maturing ectothermic organisms that depend on sandy beaches to lay their clutches of eggs, which incubate for approximately two months, at the mercy of environmental conditions (Ackerman, 1997). As clutch survival may vary across beach section (Patino-Martinez et al., 2014; e.g. from the tide line to the upper beach, Patrício et al., 2018) or between beach type (e.g. beaches with dark sand vs. beaches with white sand, Martins et al., 2020; Patino-Martinez et al., 2022), nest site selection has the potential to both enhance or reduce this parameter (Marco et al., 2018; Patrício et al.,

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* Corresponding author at: MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, 1140-041 Lisbon, Portugal.
E-mail address: apatricio@ispa.pt (A.R. Patrício).

[1] Postal address: MARE, Marine and Environmental Sciences Centre, Faculty of Sciences, University of Lisbon, Campo Grande, Lisbon 1749-016, Portugal

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2018). Thus, understanding the nest site selection behavior and its consequences for clutch survival is fundamental, particularly for populations of conservation concern.

The North East Atlantic subpopulation of loggerhead sea turtles (*C. caretta*), is listed as Endangered by the IUCN Red List of Threatened Species (Casale and Marco, 2015). Recent findings suggest a higher number of loggerhead turtles nesting in Cabo Verde than previously estimated, and that this might be the largest nesting subpopulation of this species globally (Patino-Martinez et al., 2021). However, the vast majority of the nests are concentrated in the Cabo Verde archipelago, making this subpopulation particularly vulnerable to habitat loss and degradation (Casale and Marco, 2015). Within Cabo Verde, Maio Island, hosts an important proportion of the nests, with an estimate of 4063 to 14,364 nests per year, between 2016 and 2019 (Patino-Martinez et al., 2021). The nesting beaches of Maio Island are heterogeneous in sand coloration; with light, mixed and dark sand, and loggerhead sea turtles nest on all of them. Sand color is highly correlated with sand temperature, as darker sand is warmer due to higher heat absorption associated with lower albedo (Hays et al., 2001). Since incubation temperature directly affects embryo mortality and sex (Yntema and Mrosovsky, 1982), thermal conditions impact reproductive success. Environmental temperatures can also affect the ecology (e.g. behavior, activity and distribution) of other organisms within the ecosystem, possibly altering predator-prey relationships, or the colonization capacity of pathogenic microorganisms (e.g. fungi, Sarmiento-Ramírez et al., 2014, 2010).

In Cabo Verde, the main sea turtle egg and hatchling predator is the ghost crab *Ocypode cursor* (Marco et al., 2011, 2015). Ghost crabs are ectothermic organisms highly dependent on gill moisture and susceptible to water loss by evaporation (Weinstein et al., 1994), thus sand temperature likely influences their distribution. Additionally, ghost crabs of the species *O. cursor*, being generally pale to yellowish, may lose their mimicry ability in darker sand colorations, becoming more vulnerable to predation or even be seen by their preys. Although there is not a clear pattern, studies suggest that both their distribution and level of predation on loggerhead clutches may vary across different thermal conditions (Watson et al., 2018; Tiralongo et al., 2020).

This study aimed for a better understanding of the influence of ghost crab predation on the reproductive success of loggerhead sea turtles at Maio Island, Cabo Verde, across different thermal habitats. We explored the following questions: 1) assuming that hatching success is lower in darker and warmer beaches (Martins et al., 2020; Patino-Martinez et al., 2022, studies from Cabo Verde), is such reduced embryo survival compensated by lower ghost crab predation?, and 2) do loggerhead turtles in Maio avoid nesting on beaches with either higher ghost crab density or predation? This study will contribute with recommendations for management strategies seeking to enhance sea turtle clutch survival, useful for Maio Island and similar sites, globally.

2. Material and methods

2.1. Study site and sampling period

The Cabo Verde Archipelago is located ca. 500 km west of the Senegalese coast and comprises 10 volcanic islands and some islets. This study was conducted at Maio Island (15.2° N, 23.1° W, Fig. 1) where loggerhead turtles nest in beaches of varied sand colorations, which henceforth we will refer to as 'beach type' (i.e. dark sand, mixed sand and light sand, see Fig. 1 for beach locations and names). Fieldwork took place during the loggerhead nesting season (mid-June to mid-October), in 2016 and 2017, however, we did not collect the same data in both years. Ghost crab surveys were conducted in 2016 and in 2017, but due to logistic issues, not all nesting beaches were surveyed in both years. Monitoring of loggerhead nests and nesting activities was only conducted in 2016. Lastly, in 2017, but not in 2016, we measured sand temperatures to validate the thermal differences between different sand colorations. Data collection methods are detailed below. This study was conducted under the permits of the Direcção Nacional do Ambiente - DNA and supervision of the Fundação Maio Biodiversidade, Cabo Verde. No animal experiments were performed for this study.

2.2. Ghost crab (*O. cursor*) surveys

In 2016 and 2017, we calculated the density of ghost crab burrows (burrows/m^2) within sampling transects along loggerhead nesting beaches, and measured the diameter of burrows with a scale of 15 cm (± 0.1 cm), to use these parameters as proxies for ghost crab density and size distribution, respectively. This indirect method of burrow counting and measuring to assess ghost crab density and size has been validated before (Valero-Pacheco et al., 2007; Barton and Roth, 2008; Marco et al., 2015; Oliveira et al., 2016). We randomly placed 2 m wide transects,

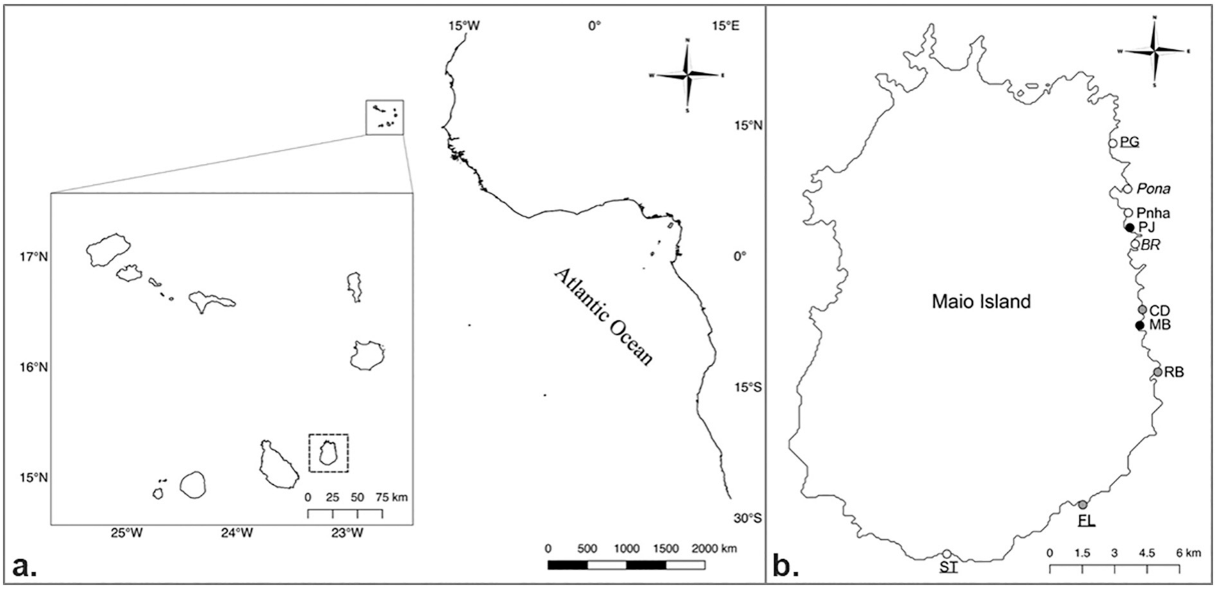

Fig. 1. a. Location of the Cabo Verde archipelago (solid frame) and of Maio Island (dashed frame); **b.** location of loggerhead nesting beaches surveyed in this study: light sand beaches (white), mixed sand beaches (grey) and dark sand beaches (black). Names in italic indicate beaches only surveyed in 2016, names underlined indicate beaches only surveyed in 2017. Remaining beaches were surveyed in 2016 and 2017.

from the high tide line to the supra-littoral dune zone. The length of transects depended on high tide amplitude and beach width, and was measured to calculate transect area (transect length x 2 m), in order to allow the estimation of mean relative density of ghost crab burrows (i.e. number of burrows/transect area). Ghost crabs are mainly reported as being nocturnal (Strachan et al., 1999; Schlacher and Lucrezi, 2010), which was also observed at Maio Island (Martins, *pers. obs.*), so we conducted surveys during the first 2 h of sunlight, after the peak of ghost crab activity, to reduce the risk of external events (e.g. human trampling, wind, high tide) affecting burrow detection. We classified burrows with diameter ≥ 2 cm as large, and assessed the density and size distribution of large burrows, as the size of individuals is highly correlated with burrow size (Marco et al., 2015; Rodrigues et al., 2016), and this is the burrow size defining potential predators of eggs and hatchlings (Frederico, 2013). In 2016, seven nesting beaches were monitored corresponding to three beach types: light ($n = 3$); mixed ($n = 2$), and dark (n = 2). In 2017 eight nesting beaches were monitored: light (n = 3); mixed (n = 3) and dark (n = 2). Two of the seven beaches surveyed in 2016 were not surveyed in 2017, and 3 new beaches were surveyed in 2017 (Fig. 1). The number of transects per beach varied according to beach length, and the distance between transects within beach was on average 25 m, with a mean of 6 ± 1 SD transects per beach in 2016 and 4 ± 3 SD in 2017. In 2016, we surveyed each beach for 10 days, with an average interval between surveys of 5 days, while in 2017 the number of surveys varied from 2 to 8. See Table S.1 for details on sampling effort.

2.3. *Nest monitoring*

In 2016, 70 nests (10 per beach) were monitored from the day of oviposition until hatchling emergence or nest failure, to evaluate the impact of ghost crab predation. The number of eggs was counted during oviposition, except for nine nests, where oviposition was not observed, and we excavated these to count the eggs. In these cases, nest excavation was conducted within a maximum of 6 h after oviposition and eggs were handled one by one, avoiding rotation, to prevent impacting embryo survival (Limpus et al., 1979).

The nests were monitored daily for inundation and erosion events (i.e. loss or gain of sand, water runoff, submersion, partial inundation, and total dragging to the sea), nearby activity by large ghost crabs (i.e. number of burrows with ≥2 cm diameter within a range of 1 m from the nest), predation by other species, human impact (e.g. nest excavation), and hatchling emergence (number of hatchlings or crawls). Each day, after data recording, all predation signs were erased to avoid double counting. Nests were considered as inundated if they were subjected to an inundation event at least once during the incubation period.

Nest exhumation was carried out five days after the last big hatchling emergence or at the end of 60 days of incubation, if no evidence of hatchling emergence was observed. The numbers of (a) dead and alive hatchlings in the egg chamber, (b) egg shells, (c) dead and alive pipped hatchlings and (d) unhatched eggs were recorded. Alive pipped hatchlings within the nest were considered hatched eggs, along with dead and alive hatchlings, while dead pipped hatchlings were categorized as unhatched eggs.

In addition, 23 clutches laid in inundation areas were translocated to a light sand hatchery (see translocation procedure in Marco et al., 2015), and left to incubate under controlled conditions, where predation, erosion and inundation were avoided, and monitored in the same way as in situ nests.

2.4. *Ghost crab impact on reproductive success*

Two parameters were considered to assess predation impact: clutch mortality and the number of stolen eggs during incubation. Clutch mortality was estimated as the sum of unhatched eggs and dead hatchlings within the nest divided by clutch size. Mortality was divided into two sources: ghost crab predation and other causes. Other causes included all mortality sources other than ghost crab predation, not assessed in this study. Ghost crab predation (P%) = ((n egg shells with evidence of ghost crab predation + n unhatched eggs with evidence of ghost crab predation + n stolen eggs) / clutch size)) x 100; and other causes (O%) = ((n unhatched eggs with no signs of ghost crab predation + n dead pipped hatchlings with no signs of ghost crab predation + n dead hatchlings inside the nest) / clutch size)) x 100. Predated eggs were distinguished by the presence of small holes in the shell characteristic of ghost crab activity.

To estimate the number of eggs stolen by ghost crabs, we used the variation of the egg number during incubation, which we calculated by subtracting the number of eggs counted after emergence to the number of eggs counted at the time of oviposition.

Importantly, in in situ nests, the variation of egg number may result from counting error during oviposition plus the eggs stolen by ghost crabs. We considered the variation in egg number from the nests incubated at the hatchery as a control, since no predation occurs at the hatchery, thus egg number variation was only due to counting error.

2.5. *Nest site selection*

To better assess the implications of ghost crab distribution and predation on the reproductive success, we calculated the nesting success and the density of both nesting activities (i.e. female emergences) and nests per beach and beach type. Nesting success was calculated by dividing the number of nests by the number of nesting activities. Density of nesting activities was calculated by dividing the number of female emergences (identified through observation of ascending and descending beach crawls) by nesting beach area. Nest density was calculated as the number of clutches divided by beach area.

2.6. *Sand temperature assessment*

To assess if sand temperature varied between beach type, we deployed temperature data loggers (Hobo Stow Away Tidbit v2 www.onsetcomp.com, temperature accuracy ±0.2 °C), recording temperature every 30 min in three beaches, each corresponding to a beach type. Loggers were buried at 27 cm depth, which was observed to be the mean burrow depth at Maio (Patino-Martinez *pers. obs.*), slightly above the mean ghost crab burrow depth measured at Boa Vista Island (range: 2.2 cm to 108 cm, mean: 19.98 cm ± 0.6 SE, (Rodrigues et al., 2016)). We confirmed data logger integrity by deploying these simultaneously for periods of 48 h at a constant temperature room before and after data collection. If loggers returned data that differed from the group mean by more than 0.5 °C, we removed them from the study. Sand measurements were conducted only throughout the 2017 nesting season.

2.7. *Statistical analyses*

To assess if there were significant differences in the density and size distribution of large ghost crab burrows across beach type and years, we fitted linear mixed effects models to the dataset, using the function *lmer* from the *lme4* package (Bates et al., 2007), with either burrow density (burrow/m^2) or burrow size (cm) as the response variable, year, beach type and the interaction between year and beach type as fixed effects and beach as a random effect. To investigate if mortality sources varied significantly between beach type we fitted generalized linear mixed effects models (GLMER), from package *lme4*, with Poisson error structure, with the probability of predation (no eggs predated per clutch) and the probability of mortality by other causes (no dead eggs/hatchlings with no evidence of predation per clutch) as the response variables, beach type as the predictor variable, beach as a random variable and clutch size as an offset. We tested for significant effects of the models using function *Anova* from the *car* package (Fox et al., 2013) with type-II sums of squares, which are more robust for unbalanced designs (Lewsey et al., 2001; Smith and Cribbie, 2021), using F-tests for the linear mixed effects models and Wald Chi-square for the generalized linear mixed effects models, followed by post hoc pairwise comparisons of beach type, with Tukey-adjusted *p*-values, implemented through package *emmeans* (Lenth et al., 2019). Residual plots were visually inspected to detect large deviations from normality. For an assessment of nest site preference, we estimated if the distribution of nests and of nesting activities were arbitrary across the available beaches, using the Chi-square test. We pooled the sand temperatures by day to eliminate extreme values and used a non-parametric Kruskal-Wallis test, for non-normal distributed data (observed by visual inspection of histograms and *qqplots*), to test if sand temperature significantly varied between beach type, followed by a Dun test with Benjamini-Hochberg adjusted *p*-values. Statistical analyses were conducted using R v.4.1.2 (http://www.r-project.org). Estimates are presented as mean ± SD, unless stated otherwise.

3. Results

3.1. Ghost crab density and size distribution

We did not find support for statistically significant effects of year ($F_{(1,11)} = 1.176$, p-value = 0.309), beach type ($F_{(2,\ 7)} = 3.328$, p-value =0.097,) or the interaction between year and beach type ($F_{(2,11)} = 0.670$, p-value = 0.530) on the density of large ghost crab burrows (Table S.3). Of the total ghost crab burrows measured in both years ($n = 6624$), 12.9% were classified as large burrows (≥ 2 cm diameter). Overall mean ghost crab burrow size was 3.1 cm ± 0.5 ($n = 493$, Table S.2). There was no support for statistically significant effects of year ($F_{(1,11)} = 1.700$, p-value = 0.151) or the interaction between year and beach type ($F_{(2,7)} = 1.700$, *p*-value = 0.223) on burrow size. The p-value for the effect of beach type on ghost crab burrow size was marginally significant ($F_{(2,7)} = 5.759$, *p*-value = 0.032), and the post hoc test indicated that this marginally significant difference was observed between light and mixed sand beaches in 2016 (*p*-value = 0.037), but not for other pairwise comparisons (Table S.3).

3.2. Ghost crab predation

Of the initial clutches monitored, 11 suffered 100% mortality due to inundation (Table 1), so we monitored 59 clutches for the predation analysis. Of these, 67.8% were attacked by ghost crabs at least once during the incubation period, with 15.0% of them being fully predated, with no eggs left (6 of the 59 assessed nests, Table 1). The mortality sources varied between beaches and beach type. The dark sand beaches had the highest clutch mortality (78.91% ± 21.26%, $n = 17$, Fig. 2). As expected, the clutches incubated in the hatchery had the lowest mortality (24.06% ± 14.15%, $n = 23$). Ghost crab predation was higher at both dark sand beaches (Pajoana and Monte Branco) and at one of the three light sand beaches (Praiona), while the other two light sand beaches had low ghost crab predation (Fig. 2). Both mixed sand beaches (Ribeira Baía and Calheta Dama) registered the lowest mortality by ghost crab predation, but suffered the highest mortality by 'other causes', along with a dark sand beach (Monte Branco, Fig. 2). The remaining beaches had lower mortality by other causes (Fig. 2). We found significant differences in ghost crab predation between beaches ($\chi^2_2 = 26.366$, *p*-value = 1.883×10^{-6}). The pairwise comparisons suggested significant differences between dark and mixed sand beaches (p-value <0.0001), and between light and mixed sand beaches (p-value = 0.003), while between dark and light sand beaches the p-value was marginally significant (p-value = 0.057, Table S.4). Mortality by other causes was higher at both mixed sand beaches (Fig. 2), but our models did not suggest significant differences between beach types ($\chi^2_2 = 4.888$, p-value = 0.087).

The ghost crab was the only egg predator detected during this study, with zero nests being directly affected by human action or by other species. Mean variation of egg count (between oviposition and emergence) was very low in hatchery nests (1 ± 2.8 eggs, n = 23; Fig. 3), which are safe from predation, suggesting that the counting error can be eliminated when carried out a group average. Considering this, the mean variation of egg count in groups of in situ nests was assumed to be a result of eggs being stolen by ghost crabs. The beaches with higher number of stolen eggs were the two dark sand beaches (Pajoana and Monte Branco) and one light sand beach (Praiona, Fig. 3). The number of stolen eggs at both mixed sand beaches was negligible (pooled 4 ± 9 eggs, $n = 18$, 0 to 24 eggs, Fig. 3).

As mentioned above, 11 of the initially monitored nests suffered 100% mortality due to inundation, but in total 52.9% ($n = 70$) of the nests were flooded at least once during the incubation period. Pajoana, a dark sand beach, had all of its nests flooded at least once during the incubation period, with complete clutch loss on 30% of the nests ($n = 10$). Boca Ribeira, a light sand beach, had the highest mortality by inundation, as five out of six flooded nests were washed to the sea by brook streams (see Table 1). Mortality of clutches that partially survived but suffered at least one inundation event was 58.7% (SD ± 23.6%, $n = 20$, 14.3 to 93.8%).

3.3. Nest site selection

During the 2016 nesting season, 2714 loggerhead nesting activities were recorded on the seven surveyed beaches, with a mean nesting success of 47.5% (Table 2). The distribution of nesting activities was not random across beaches ($\chi^2_6 = 1453$, $p < 2.22 \times 10^{-16}$), with the two mixed sand beaches having disproportionally more nesting activities than expected according to beach area (Table 2). Accordingly, nesting density was also higher at mixed sand beaches , and lower at the dark sand beaches and at the light sand beach Praiona (Table 2). When comparing by beach type, nesting activities and nest density were significantly lower than expected at the dark sand beaches (0.73/m^2; 0.27/m^2), while the mixed sand beaches had significantly more nesting

Table 1
Fate of loggerhead turtle clutches in seven beaches with different sand coloration (beach type), at Maio Island, Cabo Verde, during the nesting season of 2016. N_1: number of nests initially monitored. N_2: number of nests monitored for ghost crab predation impact (i.e., number of initially monitored clutches minus the number of clutches completely lost to flooding). See table S1 for complete beach names. Flooded and predated clutches suffered at least one event of flooding or ghost crab predation, respectively, while complete clutch loss implies 100% mortality.

Beach type	Beach	N_1	Flooded clutches	Complete clutch loss to flooding	N_2	Predated clutches	Complete clutch loss to predation
Dark	MB	10	30.0%	0%	10	70.0%	10.0%
	PJ	10	100%	30.0%	7	100%	42.9%
	Total	**20**	**65.0%**	**15.0%**	**17**	**82.4%**	**23.5%**
Mixed	CD	10	10.0%	10.0%	9	22.2%	0%
	RB	10	50.0%	10.0%	9	66.7%	0%
	Total	**20**	**30.0%**	**10.0%**	**18**	**44.4%**	**0%**
Light	BR	10	60.0%	50.0%	5	40.0%	0%
	Pnha	10	70.0%	10.0%	9	56.0%	0%
	Pona	10	50.0%	0%	10	100%	20.0%
	Total	**30**	**60.0%**	**20.0%**	**24**	**70.8%**	**8.3%**

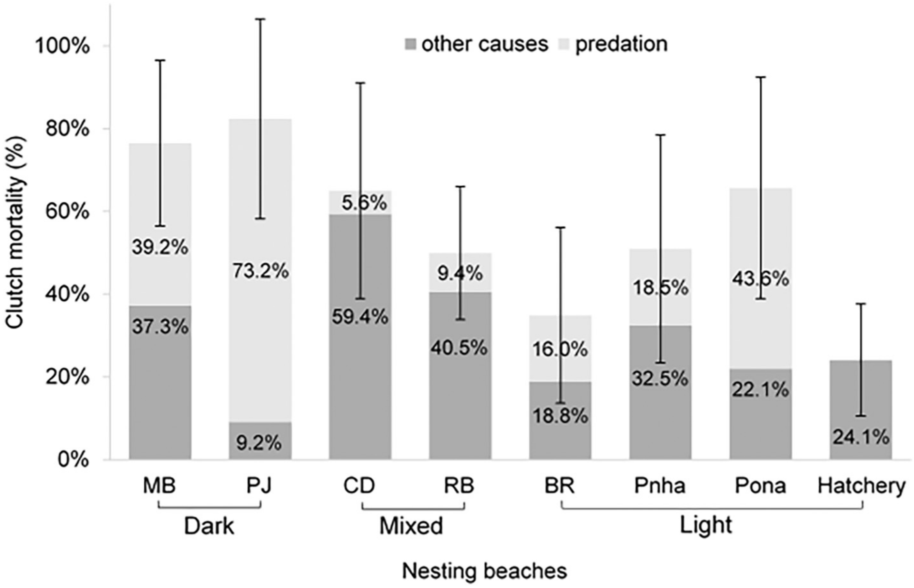

Fig. 2. Mean clutch mortality rate of the seven monitored beaches and the light sand hatchery. Each bar comprises the impact of predation (light grey) and the impact of other causes (dark grey) on overall mortality. Note that clutch mortality at the hatchery only includes other causes than predation, since no predation events were registered there. The error bars represent the standard deviation of mean overall clutch mortality rate.

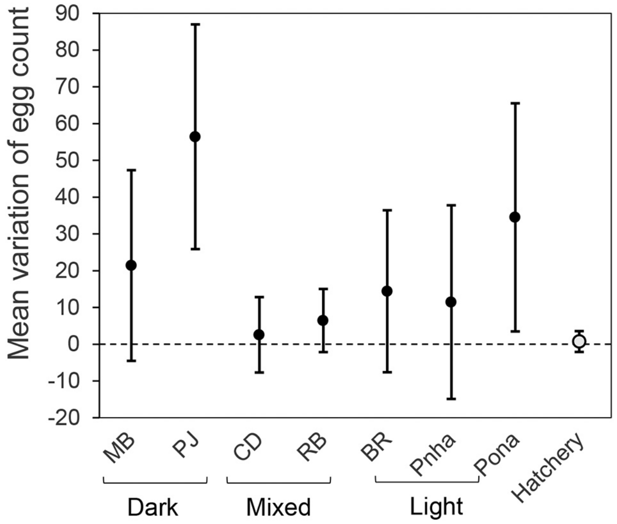

Fig. 3. Mean variation of loggerhead egg count during incubation at seven monitored beaches ($n = 59$) and at a light sand hatchery ($n = 23$) at Maio Island, Cabo Verde. Marker indicates mean, error bars represent standard deviation.

activities and nests than expected, by beach area (2.29/m^2; 1.25/m^2, respectively; $\chi^2_6 = 1099.3$, $p < 2.22 \times 10^{-16}$; Table 2).

3.4. Sand temperature

Sand temperatures differed significantly between beach type, (27 cm: χ^2_2 =157.14, *p*-value <2.2 × 10^{-16}), and between all pairwise comparisons (dark - light: Z = 12.41, p-value <0.001; dark - mixed: Z = 4.69, $p < 0.001$; mixed - light: Z = − 7.72, p-value <0.001). The dark sand registered the highest temperature, on average 1 °C higher than the mixed sand and 2.5 °C higher than the light sand (Fig. 4).

4. Discussion

The present study assessed for the first time the impact of ghost crab predation on the reproductive success of loggerhead sea turtle nests along different thermal habitats linked to different beach sand colorations present in Maio Island, Cabo Verde. Notably, this heterogeneity in beach sand coloration is also present in other important sea turtle rookeries (e.g. Ascension Island and Cyprus, Hays et al., 2001), thus this study can have a broader application. Our findings contribute to a better understanding of the interactions between ghost crab clutch predation and sand coloration, as well as introducing new questions that merit further investigation.

4.1. Ghost crab density and size distribution across different thermal habitats

Mean sand temperatures at the light sand beaches were comparable to Alagadi beach in Cyprus (29.5 °C - 33.2 °C, 30 cm depth, Godley et al., 2001), Merrit Island, Florida (24.7 °C – 30.0 °C, 37 cm depth, Mcgehee, 1979) and Fethiye beach, Turkey (26.8 °C - 31.8 °C, 44 cm depth, Kaska et al., 2006). As expected, the dark sand beaches had higher mean sand temperatures than the light and the mixed sand beaches, similar to what was shown in Ascension Island and Cyprus (Hays et al., 2001) and in eastern Australia (Limpus et al., 1983; Hays et al., 2001).

Ghost crabs are conspicuous invertebrates and their activity is highly affected by temperature (Corrêa et al., 2014), however, little is known about their thermal ecology and their spatial distribution among beaches with different thermal features as the ones we assessed in this study. Here, we used density and diameter of ghost crab burrows as proxies for ghost crab density and size (Valero-Pacheco et al., 2007; Marco et al., 2015; Oliveira et al., 2016). Despite warmer dark sand beaches likely having higher evaporation rates, which could potentially limit the activity of ghost crabs (Lucrezi and Schlacher, 2014), we found no consistent trend on ghost crab density and size structure towards any beach or beach type across years, which is in line with Patino-Martinez et al. (2022).

findings using infrared cameras to monitor ghost crab presence per night. Our findings thus suggest that the observed differences in sand temperature between beach types were not sufficient to affect these parameters, likely because the temperatures experience by ghost crabs are within their thermal range. Alternatively, ghost crabs may have behavioral adaptations to withstand warmer and drier conditions. Several thermal adaptations, such as digging deeper burrows, spending

Table 2

Summary information of loggerhead nesting activities on seven loggerhead nesting beaches, in Maio Island, Cabo Verde. Beach type refers to sand color. See table S.1 for complete beach names. Expected values were obtained by multiplying the total observed values by the area proportion. Both variables, nesting activities and nest density by beach area, were significantly different from a random distribution ($\chi2 = 1453$, df = 6, p-value < 2.2 × 10–16 and $\chi2 = 1099.3$, df = 6 p-value < 2.2 × 10–16, respectively). Symbols show the variation of the observed values compared to expected ones: observed values >50% higher (++), > 20% higher (+); within a range of 20% (=); at least 20% lower (−) < 50% (−-) than the expected values. See table S1 for beach names.

Beach type	Beach	Nesting area (m^2)	Nesting success	Nesting activities by area				Clutches laid by area			
				Expected	Observed		density (no./m^2)	Expected	Observed		density (no./m^2)
	MB	592	0.34	612	580	=	0,98	290	197	−	0,33
Dark	PJ	190	0.43	196	88	−	0,46	93	38	−	0,20
	CD	316	0.47	327	441	+	1,40	155	208	+	0,66
Mixed	RB	239	0.58	247	759	++	3,18	117	439	++	1,84
	BR	361	0.42	373	358	=	0,99	177	152	=	0,42
Light	Pnha	314	0.53	325	264	−	0,84	154	139	=	0,44
	Pona	613	0.51	634	224	−	0,37	301	115	−	0,19
Total		2625	0.47*								

* Mean nesting success across all beaches.

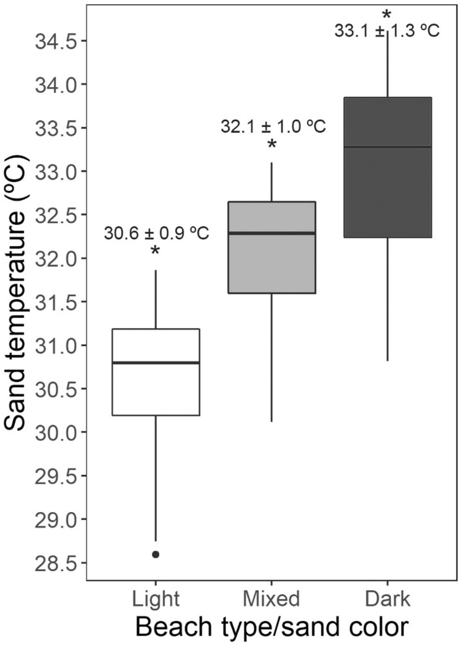

Fig. 4. Sand temperature registered on three different sand coloration beaches at a depth of 27 cm. Colors indicate sand coloration type. Boxes show median, upper and lower quartiles, whiskers show higher and lowest observations. Mean ± SD represented above each whisker.

less time on the surface, or having a spatial range closer to shore, may be adopted as an optimization to extremely hot environments. Burrows represent a stable environment for ghost crabs to cope with environmental hazards (e.g. extreme temperatures and low moisture), while offering protection from predators (e.g. raccoons and crows, Lim et al., 2011). Temperatures at burrow depth have been reported to be lower and more stable than at the surface (Chan et al., 2006; Watson et al., 2018). Additionally, larger ghost crabs are able to burrow deeper to follow the water table level of the beach, which allows them to adapt to drier conditions (Strachan et al., 1999; Tureli et al., 2009). To better understand our results, more research is needed. Future research on ghost crab physiological features (e.g. upper thermal tolerance limits, resting metabolic rate), foraging behaviors (Weinstein, 1998), burrowing dynamics (i.e. shape, depth, Chan et al., 2006; Tureli et al., 2009; Watson et al., 2018), and patterns of sea-to-shore axis distribution at different beaches (Strachan et al., 1999; Rodrigues et al., 2016) would be an important step to understand the thermal ecology of ghost crabs, also contributing to a better understanding of their interactions with sea turtle clutches.

4.2. Ghost crab predation

In Maio Island, the predation by ghost crabs has a significant impact on the reproductive success of loggerhead turtles, as our study shows that 68% of the clutches laid at the main loggerhead nesting sites are at some point predated, with 15% suffering full predation (i.e. 100% egg mortality). This result was slightly higher than the one estimated by Patino-Martinez et al. (2021) combining several Maio Island beaches but was, however, less impacting than what has been reported in Boa Vista Island, where 98% of clutches were attacked by ghost crabs at the highest-density nesting area (Marco et al., 2015). Predation levels were significantly higher at dark sand beaches, so it does not seem that potentially reduced embryo survival at these warmer beaches (Martins et al., 2020; Patino-Martinez et al., 2022) may be compensated by lower ghost crab predation. A putative explanation for the observed predation levels at dark sand beaches is linked to the negative impact of temperature on sea turtle clutches. Although the impact of temperature on clutch survival was not evaluated in this study, we observed that the dark sand beaches registered an average diel sand temperature of 33.9 °C between August and September (range 31–36 °C), and temperatures above 33 °C for long periods have been shown to compromise embryonic development and increase clutch mortality (Yntema and Mrosovsky, 1980; Matsuzawa et al., 2002; Segura and Cajade, 2010). Clutches on those beaches potentially experienced higher embryo mortality and the scent of dead eggs may be more easily detected by ghost crabs, as they have an acute sense of smell (Wellins et al., 1989; Lucrezi and Schlacher, 2014). Flood-induced egg mortality could also have contributed to increasing the scent of dead eggs, however this was observed at other beach types as well. Since we did not assess the ability of ghost crabs to detect the scent from clutches incubating at different thermal profiles, this remains a speculation. And notably, one of the light sand beaches also suffered high levels of predation, so other factors, aside from temperature, are likely to be involved. Interestingly, the mixed sand beaches, where ghost crab predation was the lowest, are the most used for fishing activities, often using ghost crabs as baits. This environmental pressure may reduce ghost crab activity and consequently predation, something to assess in the future. On the other hand, the presence of carcasses of by-caught sharks at some of these beaches (particularly at Ribeira Baía, a mixed sand beach, Martins, *pers. obs.*), may provide an alternative food source for ghost crabs, as they are generalists and opportunistic feeders, which may result in reduced loggerhead clutch predation (Lucrezi and Schlacher, 2014).

4.3. *Mortality by other causes*

Mortality by causes other than predation was considerable in some of the surveyed beaches, for instance, at both the mixed sand beaches, where predation had a low impact. Although we do not know what were the mortality causes at these beaches, upon nest exhumation, we observed several eggs with distinctive markings of fungal infection, similar to those identified by Sarmiento-Ramírez et al. (2014) in Boa Vista Island. In comparison, at the dark sand beaches, the mortality by other causes was lower, particularly at Pajoana, where ghost crab predation was the highest. A possible explanation for this result is that ghost crabs are predating eggs that otherwise would be found dead due to other causes, such as extremely high incubation temperatures. To properly assess the direct impact of sand temperature on clutch survival across these thermal habitats, a similar study should be performed with in situ nest protection, to eliminate the predation factor. Additionally, flooding was a main mortality source at one of the white sand beaches where both predation and mortality by other causes were low. Accounting only for the clutches monitored for the predation study, this beach had the lowest clutch mortality rate; however, half of the initially monitored nests were washed away either by stream brooks after rainfall, or by high tides, precluding further monitoring for predation analysis. Although the impact of inundation on egg mortality was not the aim of this study, we found it to be a serious threat that must be accounted for when assessing the reproductive output of loggerhead turtles at Maio, and when planning mitigation measures, as it contributed to 28.6% of all clutch mortality in our study site.

4.4. *Nest site selection*

We found an association between predation rate and nesting density: nesting females tended to nest less on dark sand beaches and at Praiona (light sand with high predation), and more at the mixed sand beaches, where predation was the lowest. This appears to be a reproductive advantage over crab-associated mortality. Several studies suggest that sea turtles follow environmental cues to select their nesting site, such as sand moisture, temperature, elevation above the water level, and presence of vegetation (Wilson, 1998; Wood and Bjorndal, 2000; Miller et al., 2003; Hawkes et al., 2009). Hypothetically, nesting females may have the ability to choose beaches with less predatory prevalence, based on environmental cues that have not been identified. This opens a door to further investigation on this subject.

4.5. *Conservation implications and limitations*

This study reinforces the potential role of clutch protection as a conservation measure, to reduce impacts such as predation and inundation. It also brings awareness to new research lines that merit further investigation. A study on the thermal tolerance range of ghost crabs and on their ability to detect the scent of decomposing eggs and embryos would be helpful to better understand their ecology and predict interactions with sea turtle clutches. Our study had some limitations due to an unbalanced sample design, and we recommend that the effect of sand color on clutch predation should be further explored in a multi-year study for more robust conclusions.

Maio Island represents a great input for the loggerhead Northeast Atlantic subpopulation (Patino-Martinez et al., 2021) and, given the high mortality rates among in situ clutches reported here, it is recommended that protection measures are implemented. In the past, clutches and turtles were extensively poached by local communities (Cabrera et al., 2000; Lino et al., 2010; Cozens et al., 2011; Marco et al., 2012; Hancock et al., 2017), contributing to population decline. This threat has been greatly reduced, thanks to the establishment of conservation programs (Patino-Martinez, *pers. obs.*), and now natural threats must be addressed to increase the resilience of this population, particularly under the future threat of climate change. Multiple management techniques can be adopted to maximize conservation efforts in heterogeneous nesting areas such as Maio Island beaches. For instance, in areas subjected to flooding we recommend clutch translocation to safer zones of the upper beach or eventually to protected hatcheries, ensuring that natural beach conditions (temperature and humidity) are maintained. Considering the global warming scenarios, warmer beaches in Maio Island and in similar locations might become extreme environments for sea turtle reproductive success, affecting not only clutch survival and hatchling fitness but also leading to highly skewed female biased sex ratios (Martins et al., 2020). If eliminating ghost crab predation from the dark sand beaches increases hatching success, in situ nest protection should suffice there (Marco et al., 2015). However, if underlying mortality causes arise after the elimination of predation, translocation to a light sand hatchery might be prioritized, provided that incubation conditions are monitored to avoid causing extra biases on sex ratios (Patrício et al., 2021). These measures may interfere on some level with interspecific relationships (i.e. prey-predator) and affect trophic web dynamics, thus we only recommend such actions for endangered populations, and suggest that a risk analysis is conducted ahead with clear indicators that can be assessed post-implementation.

Author contributions

AM and RM designed the study. RM, JPM, KY conducted fieldwork. RM, ARP conducted statistical analysis and wrote the first draft of the manuscript. AM, JPM, CV contributed to sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

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References

Ackerman, R.A., 1997. The Nest environment and the embryonic development of sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology of Sea Turtles, vol. 1. CRC Press, Boca Raton, pp. 83–106.

Barton, B.T., Roth, J.D., 2008. Implications of intraguild predation for sea turtle nest protection. Biol. Conserv. 141, 2139–2145.

Bates, Sarkar, Bates, Matrix, 2007. The lme4 package. R package version 2 (1), 74.

Blamires, S., Guinea, M., Prince, R., 2003. Influence of nest site selection on predation of flatback sea turtle (*Natator depressus*) eggs by varanid lizards in northern Australia. Chelonian Conserv. Biol. 4, 557–563.

Cabrera, I., Cejudo, D., Lopez-Jurado, L.F., 2000. Human predation on marine turtles in the archipelago of Cape Verde, western Africa. In: Proc. 19th Annu. Symp. Sea Turt. Biol. Conserv. NOAA Tech. Memo. NMFS-SEFSC-443 p217.

Casale, P., Marco, A., 2015. *Caretta caretta* (North East Atlantic subpopulation). In: The IUCN Red List of Threatened Species 2015 e.T83776383A83776554.

Chan, B.K., Chan, K., Leung, P.C., 2006. Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. Hydrobiologia 560, 43–49.

Corrêa, M., Andrade, L., Costa, R., Castilho, A., Bertini, G., Fransozo, A., 2014. Vertical distribution by demographic groups of ghost crab *Ocypode quadrata* (Crustacea: Brachyura). Biologia (Bratisl). 69, 905–915.

Cozens, J., Taylor, H., Gouveia, J., 2011. Nesting activity of the loggerhead sea turtle *Caretta caretta* (Linnaeus, 1758) on Maio, Cape Verde Islands. Zool. Caboverdiana 2, 62–70.

Fox, J., Friendly, M., Weisberg, S., 2013. Hypothesis tests for multivariate linear models using the car Package. R J. 5. R J., p. 39

Frederico, A.P., 2013. Avaliação da estratégia do caranguejo-fantasma *Ocypode cursor* para a detecção e predação de ninhos da tartaruga *Caretta caretta*. In: Relatório de estágio do Curso de Licenciatura em Biologia Marinha e Pescas. Mindelo. DECM. Universidade de Cape Verde (41 pp. + annexes).

Godley, B.J., Broderick, A.C., Mrosovsky, N., 2001. Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations. Mar. Ecol. Prog. Ser. 210, 195–201.

Hancock, J., Furtado, S., Merino, S., Godley, B.J., Nuno, A., 2017. Exploring drivers and deterrents of the illegal consumption and trade of marine turtle products in Cape Verde, and implications for conservation planning. Oryx 51, 428–436.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2009. Climate change and marine turtles. Endanger. Species Res. 7, 137–154.

Hays, G.C., Ashworth, J.S., Barnsley, M.J., Broderick, A.C., Emery, D.R., Godley, B.J., Henwood, A., Jones, E.L., 2001. The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. Oikos 93, 87–94.

Kamel, S.J., Mrosovsky, N., 2005. Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. Anim. Behav. 70, 819–828.

Kaska, Y., Ilgaz, Ç., Özdemir, A., Başkale, E., Türkozan, O., Baran, İ., Stachowitsch, M., 2006. Sex ratio estimations of loggerhead sea turtle hatchlings by histological examination and nest temperatures at Fethiye beach, Turkey. Naturwissenschaften 93, 338–343.

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2019. Package ‘emmeans.’.

Lewsey, J.D., Gardiner, W.P., Gettinby, G., 2001. A study of type II and type III power for testing hypotheses from unbalanced factorial designs. Commun. Stat. - Simul. Comput. 30, 597–609.

Lim, S.S., Yong, A.Y., Tantichodok, P., 2011. Comparison of burrow morphology of juvenile and young adult *Ocypode Ceratophthalmus* from Sai Kaew, Thailand. J. Crustac. Biol. 31, 59–65.

Limpus, C.J., Baker, V., Miller, J.D., 1979. Movement induced mortality of loggerhead eggs. Herpetologica 35, 335–338.

Limpus, C.J., Reed, P., Miller, J.D., 1983. Islands and turtle: the influence of choice of nesting beach on sex ratio. In: Baker, J.T., Carter, R.M., Sammarco, P.W., Stark, K.P. (Eds.), Proceedings of the Inaugural Great Barrier Reef Conference. James Cook University Press, Townsville, Australia, pp. 397–402.

Lino, S., Gonçalves, E., Cozens, J., 2010. The loggerhead sea turtle (*Caretta caretta*) on Sal Island, Cape Verde: nesting activity and beach surveillance in 2009. Arquipelago. Life Mar. Sci. 27, 59–63.

Lucrezi, S., Schlacher, T.A., 2014. The ecology of ghost crabs. Oceanogr. Mar. Biol. Annu. Rev. 52, 201–256.

Mansouri, I., Ousaaid, D., Squalli, W., Sqalli, H., El Ghadraoui, L., Dakki, M., 2020. The turtle dove (*Streptopelia turtur*) in Midelt plain, Morocco: nesting preferences and breeding success versus the impact of predation and agricultural practices. J. Anim. Behav. Biometeorol. 8, 206–214.

Marchand, M.N., Litvaitis, J.A., 2004. Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests. Biol. Conserv. 117, 243–251.

Marco, A., Abella Pérez, E., Monzón Argüello, C., Martins, S., Araujo, S., López-Jurado, L. F., 2011. The international importance of the archipelago of Cape Verde for marine turtles, in particular the loggerhead turtle *Caretta caretta*. Zool. Caboverdiana 2, 1–11.

Marco, A., Abella, E., Liria-Loza, A., Martins, S., López, Ó., Jiménez-Bordón, S., Medina, M., Oujo, C., Gaona, P., Godley, B.J., López-Jurado, L.F., 2012. Abundance and exploitation of loggerhead turtles nesting in Boa Vista island, Cape Verde: the only substantial rookery in the eastern Atlantic. Anim. Conserv. 15, 351–360.

Marco, A., Da Graça, J., García-Cerdá, R., Abella, E., Freitas, R., 2015. Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population. J. Exp. Mar. Biol. Ecol. 468, 74–82.

Marco, A., Abella, E., Martins, S., López, O., Patino-Martinez, J., 2018. Female nesting behaviour affects hatchling survival and sex ratio in the loggerhead sea turtle: implications for conservation programmes. Ethol. Ecol. Evol. 30, 141–155.

Martins, S., Silva, E., Abella, E., Loureiro, N., Marco, A., 2020. Warmer incubation temperature influences sea turtle survival and nullifies the benefit of a female-biased sex ratio. Clim. Chang. 163, 689–704.

Matsuzawa, Y., Sato, K., Sakamoto, W., Bjorndal, K.A., 2002. Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. Mar. Biol. 140, 639–646.

Mcgehee, M.A., 1979. Factors affecting the hatching success of loggerhead sea turtle eggs (*Caretta caretta*). Master thesis. University of Central Florida, Orlando, FL.

Miller, J.D., Limpus, C.J., Godfrey, M.H., 2003. Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. In: Bolten, A.B., Witherington, B. (Eds.), Loggerhead Sea Turtles. Smithsonian Books Washington, DC, pp. 125–143.

Mortimer, J.A., 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of Green turtles (*Chelonia mydas*). Copeia 1990, 802–817.

Patino-Martinez, J., Marco, A., Quiñones, L., Hawkes, L.A., 2014. The potential future influence of sea level rise on leatherback turtle nests. J. Exp. Mar. Biol. Ecol. 461, 116–123.

Oliveira, C., Neves, G., Soares-Gomes, A., 2016. Measuring burrows as a feasible non-destructive method for studying the population dynamics of ghost crabs. Mar. Biodivers. 46, 809–817.

Patino-Martinez, J., Dos Passos, L., Afonso, I.O., Teixidor, A., Tiwari, M., Székely, T., Moreno, R., 2021. Globally important refuge for the loggerhead sea turtle: Maio Island. Cabo Verde. Oryx 1–9.

Patino-Martinez, J., Veiga, J., Afonso, I.O., Yeoman, K., Mangas-Viñuela, J., Charles, G., 2022. Light Sandy Beaches Favour Hatching Success and Best Hatchling Phenotype of Loggerhead Turtles. Front. Ecol, Evol, p. 10.

Patrício, A.R., Varela, M.R., Barbosa, C., Broderick, A.C., Airaud, M.B.F., Godley, B.J., Regalla, A., Tilley, D., Catry, P., 2018. Nest site selection repeatability of green turtles, *Chelonia mydas*, and consequences for offspring. Anim. Behav. 139, 91–102.

Patrício, A.R., Varela, M.R., Barbosa, C., Broderick, A.C., Catry, P., Hawkes, L.A., Regalla, A., Godley, B.J., 2019. Climate change resilience of a globally important sea turtle nesting population. Glob. Chang. Biol. 25, 522–535.

Patrício, A.R., Hawkes, L.A., Monsinjon, J., Godley, B.J., Fuentes, M.M., 2021. Climate change and marine turtles: recent advances and future directions. Endanger. Species Res. 44, 363–395.

Pike, D.A., Roznik, E.A., Bell, I., 2015. Nest inundation from sea-level rise threatens sea turtle population viability. R. Soc. Open Sci. 2, 150127.

Rodrigues, E., Freitas, R.P., de Delgado, N.C., Soares-Gomes, A., 2016. Distribution patterns of the ghost crab *Ocypode cursor* on sandy beaches of a tropical island in the Cabo Verde archipelago, eastern Central Atlantic. Afr. J. Mar. Sci. 38, 181–188.

Sarmiento-Ramírez, J.M., Abella, E., Martín, M.P., Tellería, M.T., López-Jurado, L.F., Marco, A., Diéguez-Uribeondo, J., 2010. Fusarium solani is responsible for mass mortalities in nests of loggerhead sea turtle, *Caretta caretta*, in Boavista. Cape Verde. FEMS Microbiol. Lett. 312, 192–200.

Sarmiento-Ramírez, J.M., Abella-Pérez, E., Phillott, A.D., Sim, J., van West, P., Martín, M.P., Marco, A., Diéguez-Uribeondo, J., 2014. Global distribution of two fungal pathogens threatening Endangered Sea turtles. PLoS One 9, e85853.

Schlacher, T.A., Lucrezi, S., 2010. Compression of home ranges in ghost crabs on sandy beaches impacted by vehicle traffic. Mar. Biol. 157, 2467–2474.

Segura, L., Cajade, R., 2010. The effects of sand temperature on pre-emergent green sea turtle hatchlings. Herpetol. Conserv. Biol. 5, 196–206.

Smith, C., Cribbie, R., 2021. Factorial ANOVA with unbalanced data: a fresh look at the types of sums of squares. J. Data Sci. 12, 385–404.

Spencer, R.J., 2002. Experimentally testing Nest site selection: fitness trade-offs and predation risk in turtles. Ecology 83, 2136–2144.

Strachan, P.H., Smith, R.C., Hamilton, D.A.B., Taylor, A.C., Atkinson, R.J.A., 1999. Studies on the ecology and behaviour of the ghost crab, *Ocypode cursor* (L.) in northern Cyprus. Sci. Mar. 63, 51–60.

Tiralongo, F., Messina, G., Marino, S., Bellomo, S., Vanadia, A., Borzì, L., Tibullo, D., Di Stefano, A., Lombardo, B.M., 2020. Abundance, distribution and ecology of the tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Ocypodidae) from a recently colonized urban sandy beach, and new records from Sicily (Central Mediterranean Sea). J. Sea Res. 156, 101832.

Tureli, C., Duysak, O., Akamca, E., Kiyagi, V., 2009. Spatial distribution and activity pattern of the ghost crab, *Ocypode cursor* (L., 1758) in Yumurtalik Bay, North-Eastern Mediterranean-Turkey. J. Anim. Vet. Adv. 8, 165–171.

Valero-Pacheco, E., Alvarez, F., Abarca-Arenas, L., Escobar, M., 2007. Population density and activity pattern of the ghost crab, Ocypode quadrata, in Veracruz, Mexico. Crustaceana 80, 313–325.

Watson, G.S., Gregory, E.A., Johnstone, C., Berlino, M., Green, D.W., Peterson, N.R., Schoeman, D.S., Watson, J.A., 2018. Like night and day: reversals of thermal gradients across ghost crab burrows and their implications for thermal ecology. Estuar. Coast. Shelf Sci. 203, 127–136.

Weinstein, R.B., 1998. Effects of temperature and water loss on terrestrial locomotor performance in land crabs: integrating laboratory and field Studies1. Am. Zool. 38, 518–527.

Weinstein, R.B., Full, R.J., Ahn, A.N., 1994. Moderate dehydration decreases locomotor performance of the ghost crab, *Ocypode quadrata*. Physiol. Zool. 67, 873–891.

Wellins, C.A., Rittschof, D., Wachowiak, M., 1989. Location of volatile odor sources by ghost crab *Ocypode quadrata* (Fabricius). J. Chem. Ecol. 15, 1161–1169.

Wilson, D.S., 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. Ecology 79, 1884–1892.

Wood, D.W., Bjorndal, K.A., 2000. Relation of temperature, moisture, salinity, and slope to Nest site selection in Loggerhead Sea turtles. Copeia 2000, 119–128.

Yntema, C.L., Mrosovsky, N., 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. Herpetologica 36, 33–36.

Yntema, C.L., Mrosovsky, N., 1982. Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. Can. J. Zool. 60, 1012–1016.