Ecological drivers of the high predation of sea turtle hatchlings during emergence

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ABSTRACT: Synchronized emergence of offspring may represent an adaptive strategy to reduce predation risk. This strategy swamps the short-term capacity of predators to consume prey before offspring disperse, inducing a dilution effect, thus improving an individual's chance of survival. In the case of sea turtles, this occurs during emergence and mass migration to the sea, to avoid potential predators on the beach. In this study, we evaluated the effect of group size on predation rates of loggerhead turtle *Caretta caretta* hatchlings during the crawl to the sea on Boa Vista Island, Cabo Verde. Our results show that synchronous emergence reduced rates of predation by tufted ghost crabs *Ocypode cursor*. The mean estimated predation rate overall was 50.3%. Predation was highest (~75%) in the smallest group sizes and decreased to ~25% in larger groups, due to the lower probability of an individual being attacked by a ghost crab. Our observations also indicate significantly higher predation rates at night (55%) than during the day (22%). No relationship between predation rates and the distance between the nest and the surf zone of the sea was identified; however, this is likely due to the behaviour of ghost crabs, i.e. waiting close to the tide line for hatchlings during the night. Our results provide important information for the management and conservation of endangered sea turtle populations in areas with high densities of predatory ghost crabs. Specifically, to reduce predation rates, we recommend that hatchlings are released in large groups at twilight hours and in areas of low ghost crab densities.

KEY WORDS: Sea turtles · Loggerhead · *Caretta caretta* · Synchronous emergence · Predation risk · Ghost crab · Ocypodidae · *Ocypode cursor* · Cabo Verde

1. INTRODUCTION

In the wild, many species demonstrate behavioural synchrony during a particular life stage that may improve fitness (Tucker et al. 2008, Furey et al. 2016, Descamps 2019). Such benefits can include more efficient reproduction, improved food acquisition, increased movement efficiency and defence against potential predators. In particular, it is thought that predator avoidance is a major factor in the evolution of synchronized behaviour in many species (Ims 1990, O'Donoghue & Boutin 1995, Spencer et al. 2001, Santos et al. 2016, Descamps 2019). However, in larger groups, this behaviour can become costly for individuals, for example by increasing within-group competition for food (Isbell 1991) or increasing

the probability of detection by predators (Dehn 1990, Reising et al. 2015, Wilson et al. 2019).

Previous studies have suggested that species that synchronize the emergence of offspring display this behaviour in order to swamp the short-term capacity of predators to consume them before they disperse, inducing a dilution effect and thus improving an individual's chance of survival (Treherne & Foster 1982, Clark & Mangel 1986, Ims 1990, Spencer et al. 2001, Tucker et al. 2008, Furey et al. 2016, Santos et al. 2016). For instance, this synchronicity has been observed in the aggregation of a marine insect, *Halobates robustus* (Treherne & Foster 1982), in the emergence of cicadas *Magicicada* sp. (Williams et al. 1993), in the emergence of juvenile Atlantic salmon *Salmo salar* (Brännäs 1995) and in many species of turtles and tortoises (Eckrich & Owens 1995, Spencer et al. 2001, Tucker et al. 2008, Colbert et al. 2010, Tomillo et al. 2010, Peterson et al. 2013, Santos et al. 2016).

Sea turtles are well known for the synchronized emergence of both nesting females and of hatchlings, with the largest mortality rates occurring in the early life stages. A striking example of synchronized reproduction to potentially mitigate against this high mortality rate occurs in some populations of the genus *Lepidochelys*, a phenomenon known as the 'arribada', or 'arrival', a synchronized and large-scale nesting event of up to tens of thousands of nesting females. The predation rate on hatchlings that emerge from nests laid during these 'arribada' events has been shown to be lower compared to hatchlings from nests laid by solitary females (Eckrich & Owens 1995). This strategy facilitates group emergence from the nest and their movement towards the sea, diluting individual risk and minimising the number of potential predators that an individual hatchling may encounter (Spencer et al. 2001, Rusli et al. 2016).

Synchronized emergence in sea turtle hatchlings has an attack abatement effect, with higher group sizes (the number of hatchlings emerging simultaneously) 'swamping' terrestrial predators, reducing overall predation rates (Conant 1991, Ioannou et al. 2011, Peterson et al. 2013, Santos et al. 2016) and increasing the overall proportion that successfully reach the sea (Treherne & Foster 1982). While the vast majority of hatchlings emerge at the first event (Glen et al. 2005, Adam et al. 2007, Marco et al. 2018a), asynchronized emergences from a single nest (emergences on different nights within the same nest) have been observed across a period of 1 wk (Glen et al. 2005). Studies have hypothesised that synchronized emergence is an adaptive response to reduce predation (Spencer et al. 2001, Adam et al. 2007, Tucker et al. 2008), although few studies have empirically tested this hypothesis on sea turtles. Conversely, predation on hatchling leatherback turtles *Dermochelys coriacea* has been observed to increase with increasing number of hatchlings during the crawl to the water (Tomillo et al. 2010). Other studies have reported a similar trend, suggesting that larger hatchling groups are more likely to be detected and thus preyed upon by predators (Dehn 1990, Piltcher et al. 2000, Wyneken et al. 2000, Reising et al. 2015, Wilson et al. 2019). Few studies have experimentally evaluated how group size (i.e. the number of hatchlings emerging together from a nest) in combination with the distance of the nest from the sea influences predation on sea turtle hatchlings (Santos et al. 2016, Erb & Wyneken 2019), and the contrasting evidence on the effect of synchronous emergence warrants further investigation.

In addition, the timing of emergence can influence how group size and the time spent on the beach influence predation risk. Hatchling emergence occurs mainly during the night or at twilight to avoid lethal daytime temperatures and diurnal predators (Gyuris 1994, Drake & Spotila 2002). Daytime emergence does occasionally occur, during periods of cooler temperatures such as heavy rain or cloud cover, or as hatchlings are forced to emerge from the nest by siblings ascending from below that experience cooler temperatures (Drake & Spotila 2002, Glen et al. 2005).

Several species consume sea turtle hatchlings during their crawl from the nest to the water (Peterson et al. 2013, Erb & Wyneken 2019), although ghost crabs (*Ocypode* spp.) represent some of the most common predators that occur on nesting beaches (Simms et al. 2002, Tomillo et al. 2010, Rebelo et al. 2012, Marco et al. 2015, Santos et al. 2016). Ghost crabs are the largest and most conspicuous invertebrates and are among the fastest predators found on ocean shores. They play a key role in littoral food webs both as mesopredators and as bioturbators, and their nocturnal periods of activity coincide with hatchling emergence (Lucrezi & Schlacher 2014). Predation rates on hatchlings during migration to the sea can be significant. For example, predation on hatchling loggerhead turtles *Caretta caretta* by ghost crabs has been documented at rates of 24% in North Carolina, USA (Peterson et al. 2013), 30% in Cabo Verde in the east Atlantic (Marco et al. 2015) and over 50% in Egyptian Sinai (Simms et al. 2002). A rate of 77% predation on hatchling green turtles *Chelonia mydas* at a rook-

ery in Poilão, Guinea-Bissau, has also been reported (Rebelo et al. 2012).

In this study, we intended to determine, under natural conditions, the predation rate of loggerhead turtle hatchlings by tufted ghost crabs *O. cursor*, during their crawl to the water. Specifically, we aimed to: (1) analyse the influence of synchronized emergence on predation rates, (2) evaluate if the predation rate increases with the distance from the emergence point to the surf zone, (3) compare the rate of predation among different periods of the day (night, day and twilight) and (4) investigate the influence of predator density on predation rates. We hypothesised that synchronized emergence would increase hatchling survival, due to the dilution effect within the group members, and that predation rates would increase with greater distance from the sea due to increased time spent on the beach, and therefore higher exposure to ghost crab attacks. Furthermore, we anticipated that as ghost crabs display mainly nocturnal activity, higher predation rates would occur at night and in areas of higher predator densities. Finally, we monitored emergence patterns in order to estimate beach-wide predation rates.

2. MATERIALS AND METHODS

2.1. Study site

This study was carried out on João Barrosa beach (16° 02′ N, 22° 45′ W), a 5 km long beach on the south-

eastern coast of Boa Vista Island, Cabo Verde Archipelago, (Fig. 1). João Barrosa beach is within a Sea Turtle Natural Reserve and represents one of the most important nesting areas for loggerhead turtles in Cabo Verde, with approximately 20% of total nesting activities occurring there (Marco et al. 2012a). Cabo Verde is the only rookery of the eastern Atlantic loggerhead subpopulation, with an average number of 105 000−140 000 nests per season (Marco et al. 2012a,b, Laloë et al. 2020). The white sandy beaches where nesting occurs are characterized by a high density of ghost crabs and a lack of other predators (Marco et al. 2015). Human presence in the area is very low, with no human settlements except a field camp built annually during the nesting season (from June until October) as part of sea turtle conservation efforts. The disturbance to the beach is therefore negligible, accurately representing natural environmental conditions. All research was performed under the ethical approval of the National Directorate of the Environment of Cabo Verde (permit number: DGA, 21/2013).

2.2. Monitoring hatchling emergence patterns

During July, August and September 2013, 78 doomed clutches (i.e. clutches that were laid in areas of the beach that would certainly lead to nest failure) were relocated to a conservation hatchery located on the same beach (Fig. 1b). All 78 nests were used to determine the nest emergence pattern, and 56 nests
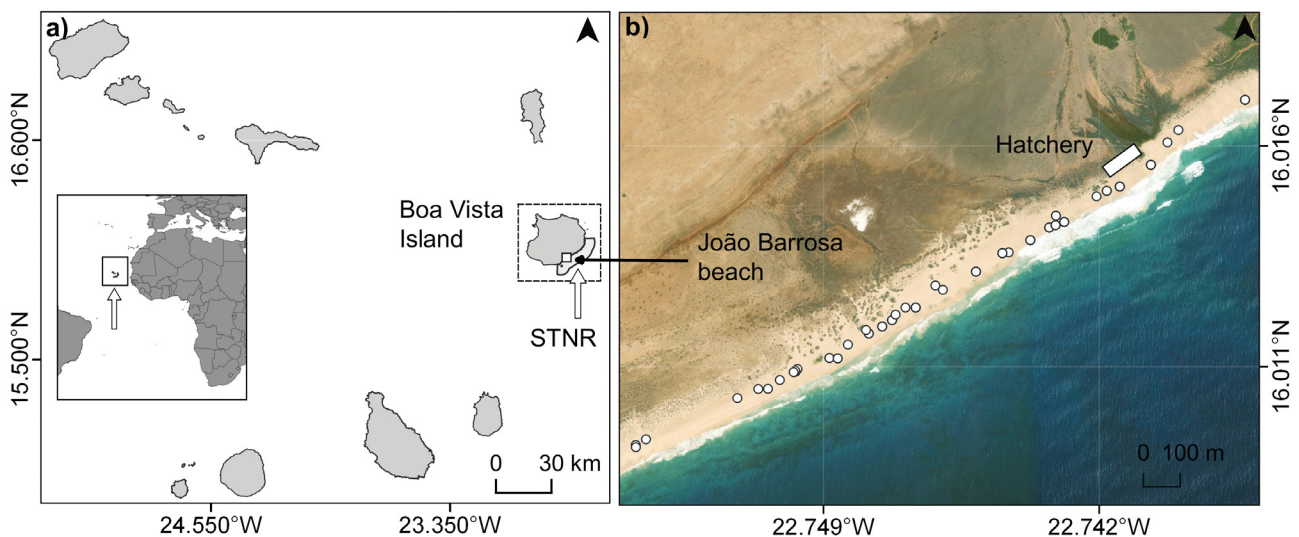

Fig. 1. (a) Republic of Cabo Verde off the West African coast, showing the island of Boa Vista with the study area (João Barrosa beach) and the boundary of the Sea Turtle Natural Reserve (STNR). (b) Aerial photo of João Barrosa beach, showing the location of the hatchery (white rectangle) and the points where loggerhead hatchlings were released (white circles)

were used to study the predation rate. The clutches were relocated immediately after being laid, using a standardised tested protocol (Abella et al. 2007, Marco et al. 2012a). Clutches were carefully reburied within standardised, hand-dug cavities that resembled natural nests in shape and size at a depth of 50 cm, the average nest depth for this population (Marco et al. 2018a). Clutches were placed 70 cm apart, with the outer clutches being located 80 cm from the edges of each section of the hatchery. A circular corral made of plastic mesh set on the sand surface above each nest retained emerging hatchlings to better understand the emergence patterns and to determine group size and to estimate average mortality rate over the beach. The reason for not using *in situ* nests was the inability to accurately monitor and record emergence. Hatchery conditions replicated the wider nesting beach and we are therefore confident that emergence patterns would not be different from those observed *in situ* (Adam et al. 2007).

Nests were monitored from sunset until dawn. The number of hatchlings in each emergence (defined as any individual or group of hatchlings observed inside the plastic mesh) was recorded, and allocated into 1 of the 6 following categories: category 1 (<3 hatchlings); category 2 (3–7 hatchlings); category 3 (8–15 hatchlings); category 4 (16–25 hatchlings); category 5 (26–40 hatchlings) and category 6 (>40 hatchlings). Emergence events in individual nests were recorded up to a maximum of 3 d. All hatchlings were released along João Barrosa beach following the guidelines of Marco et al. (2012b).

2.3. Predation study

A predation study was conducted during September, October and November 2013 using hatchlings from 56 of the relocated nests described in Section 2.2. Immediately after the first emergence, 2354 hatchlings from the 56 relocated nests were selected for this experiment, and we only used hatchlings from the first emergence to minimise any impact to an individual nest. Trials to assess predation by ghost crabs were conducted using groups of different numbers of hatchlings: 1, 5, 10, 20, 30 and 50 individuals. These numbers were in the range of those that occur in natural emergence events (Drake & Spotila 2002, Glen et al. 2005, Adam et al. 2007). All hatchlings in each individual release were from the same nest and cohort, as occurs in natural emergences, to avoid any confounding effect of releasing hatchlings from different nests simultaneously.

The methods of releasing hatchlings and observing predation rates were designed to mimic the conditions of a natural emergence as much as possible. The release points on the beach corresponded to locations of nests registered by the local NGO that monitors loggerhead nesting on that beach (Fig. 1b), thereby ensuring that the simulated hatching points were places where a natural emergence could occur. A total of 34 release points spread along a 2.5 km stretch of beach were used. Hatchlings were released over a small hole dug in the sand of about 10–15 cm depth to recreate natural conditions in which hatchlings escape the nest once the surface is reached (Fig. S1 in the Supplement at www.int-res. com/articles/suppl/m668p097_supp.pdf). Hatchlings were released no longer than 120 min after emergence within the beach hatchery (excepting during the daytime release, where the hatchlings came from the last dawn emergence).

In order to reduce the influence of human presence and to optimize behavioural observations of hatchlings and ghost crabs, 2 people jointly carried out hatchling releases and observations. Observation of predation events was taken while hatchlings were crawling from the nest to the sea using infrared binoculars where necessary. The first person released the hatchlings and made observations over the upper half of the shore while the second observed the lower half of the shore to the water line. Observers remained still and silent in their positions for 5–10 min prior to each release to minimise any confounding effect of their presence on ghost crab behaviour, after which the hatchlings were released. In cases of uncertainty, the tracks of turtles and crabs were followed after the trial to establish the fate of all hatchlings. This usually took place with larger groups of turtles and under conditions of low visibility. Once each trial was completed (typically lasting 15–20 min), preyed hatchlings were released since crabs do not kill them instantly but transport them to their burrows, and in most cases, hatchlings were not seriously harmed by the time they were retrieved by researchers. As these trials involved trampling and altering the beach area, only 1 trial per day was carried out at each individual release point.

A total of 167 trials were conducted, most of them (n = 125) at night (19:00–05:45 h), but also during twilight (n = 24; 05:45–06:15 and 18:30–19:00 h) and daytime (n = 18; 06:15–18:30 h), to investigate differences in predation rates between different times of the day. The tidal cycle can influence ghost crab activity (Lucrezi & Schlacher 2014), but the tidal range on Boa Vista is very low, with a range of <1 m

(Gomes et al. 2015), so we did not include this as a factor in our analysis. The predation rate for each trial was calculated as the percentage of all released hatchlings that were preyed upon on their way from the release point to the water.

Between each release, we measured the distance from the release point to the sea with a measuring tape. This was the approximate distance that hatchlings crawled from the nest to the water. Given the considerable variation in this measurement according to the strength and shape of each wave, it was calculated as the distance between the release point and the average point reached by waves during the trial. The distances of each release ranged between 10 and 50 m. It was not possible to conduct these trials at a greater distance due to only having 2 observers and low visibility.

The density of ghost crab holes was recorded in each release area, as a proxy for predator density. This assumption is reasonable because in the family Ocypodidae, each individual typically occupies only 1 hole (Barros 2001, Barton & Roth 2008). We calculated ghost crabs hole densities along an imaginary line from the water's edge towards the vegetation zone (the point where the open sandy beach ends) and a width of 30 m, with the release point in the centre, thereby covering the area within which release trials were conducted. We classified crab hole densities in each trial into 3 different categories: low (0–0.18 crab holes m^{-2}), medium (0.19–0.40) and high (≥ 0.45). Hatchlings were recorded as 'preyed upon' if they were taken by crabs into burrows, accidentally fell into burrows or became disoriented and did not reach the sea, as we assumed that all of these events would lead to predation of hatchlings by ghost crabs. Predation rates are presented as the percentage of hatchlings preyed upon in each group.

2.4. Data analysis

All statistical analyses were performed in R v.4.0.0 (R Core Team 2020), assuming a 5% level of significance. Trends in predation rates (i.e. the % of hatchlings preyed upon in each trial) were analysed using a generalised linear model (GLM) with a binomial error distribution, including distance to the sea as a continuous predictor variable and the categorical variables of group size and ghost crab hole density. Correlation analysis, using Pearson's correlation coefficient, was used to avoid collinearity between predictor variables. Significant differences were identified and data from daytime releases were subsequently excluded from the rest of the analysis. To run the GLM, only data

from night and twilight trials were used because in nature, this is when the majority of emergence events occur. We performed a separate analysis including the variable 'time of day', using a generalised mixed-effect model (GLMM) with a logit link function and a binomial error distribution, and included group size as a random factor. When plotting the data, the distance to the sea was grouped into 5 m bins and included as a categorical variable. We developed a list of candidate models based on the variables 'hatchling group size', 'distance to the sea' and 'ghost crab hole density'. We used Akaike's information criterion (AIC), as proposed by Burnham & Anderson (2004), to select the best model, using a forward stepwise approach, choosing the best-fitting models based on the lowest AIC values. All models with ΔAIC < 2 were assumed to have equal support for use with the data (Burnham & Anderson 2004). We also performed a non-parametric Spearman's rank correlation to better characterize the relationship between hatchling group size (included as a discrete variable) and ghost crab predation rate. A 1-way ANCOVA was conducted to determine the effect of ghost crab hole density on predation rate after controlling for group size (group size as the co-variate). Post hoc analysis was performed with a Bonferroni adjustment to identify between-group differences.

We estimated overall mortality rates across the beach using the mean mortality rate in each group size and the observed emergence patterns from 78 clutches. First, we categorized each emergence from the 78 clutches relocated to the hatchery into 1 of the 6 categories as described in Section 2.2. We then calculated the percentage of hatchlings that emerged across the entire beach in each category, and used our observed mortality rates of different group sizes to estimate overall hatchling predation rates for the wider population.

3. RESULTS

3.1. Emergence

The emergence patterns of relocated clutches was characterized by the following proportions in each category: 2.7% of all emergences were category 1 (<3 hatchlings), 4.5% in category 2 (3–7 hatchlings), 5.7% in category 3 (8–15 hatchlings), 10.9% in category 4 (16–25 hatchlings), 15.4% in category 5 (26–40 hatchlings) and 60.8% in category 6 (>40 hatchlings)(average ± SD = 61.3 ± 12.4 hatchlings). Hence, the majority of emergence events consisted of large numbers of hatchlings.

3.2. Variation in predation rates

Significant differences in hatchling predation rates were observed between times of day (Fig. 2a). Predation was markedly greater at night (mean ± SD = 54.8 ± 31.42%) than under daylight conditions (21.9 ± 32.2%; GLMM: $F = 29.043$, p < 0.001), but not significantly greater than at twilight (39.9 ± 34.9%; $F = 8.885$, p = 0.054). Predation rates during twilight were also significantly higher than during the day (GLMM: $F = 7.813$, p = 0.0063).

The mean ghost crab predation of hatchlings released in this study was of 50.3% (Fig. S2 in the Supplement), and a further 3% were disoriented or trapped in vegetation. In 6 events, we observed that ghost crabs captured more than 1 turtle in a single release event, and that 70% of captures occurred in the area between tidemarks up to 15 m inland. The best-fitting GLM for predation rate data included hatchling group size, distance to the sea and ghost crab hole density as predictor variables, and the interaction between distance to the sea and ghost crab hole density (Table 1). The model with the lowest AIC value was chosen (hatchling group size, distance to the sea and ghost crab hole density). Group size significantly influenced predation rates (GLM: $F = 79.989$, p < 0.0001), with model results indicating higher levels of predation in smaller groups and decreasing predation rates as group size increased (Spearman's $r_S = -0.65$, df = 147, p < 0.0001; Fig. 2b). Applying the observed emergence pattern of hatchlings to the wider population, the weighted average
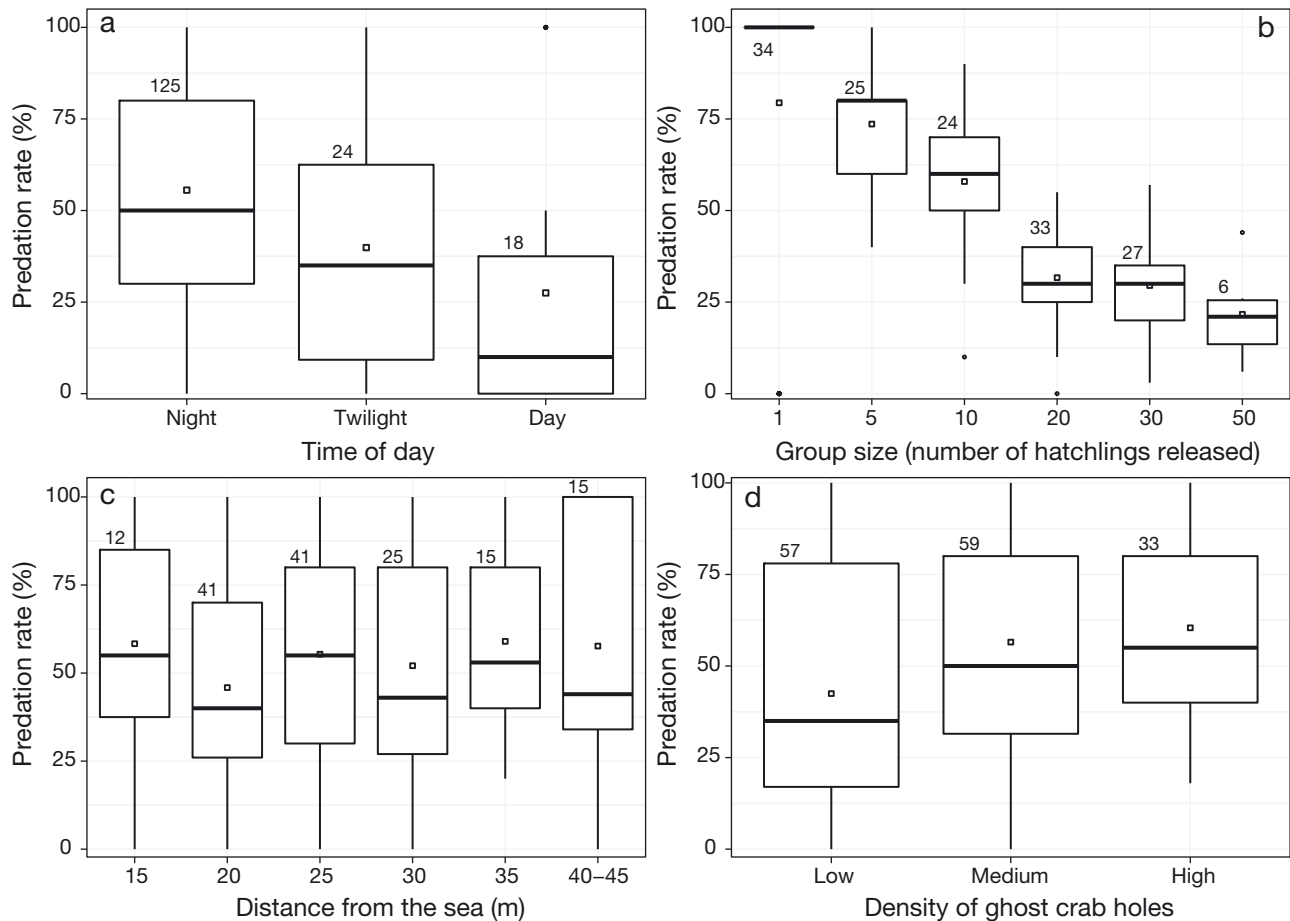

Fig. 2. Predation rate (%) of loggerhead turtle hatchlings (a) according to 3 different times of day; (b) for the different group sizes established in the study; (c) at different distances from the nest to the shoreline; and (d) according to 3 categories of ghost crab hole density. Panels b–d only include data from nighttime and twilight trials. In panel b, for the first experimental group (only 1 hatchling released), the small square indicates the percentage of single turtles preyed upon in all trials (SD = 45.0). In panel c, for better visualization of the variable 'distance to the sea', data were grouped in 5 m bins (but raw data was used in the GLM). In all panels, the white box shows the interquartile range, the solid black line shows median value, the small square is the mean, whiskers represent the minimum and maximum values, and the circles show statistical outliers. Sample sizes (i.e. experimental runs) are noted above each boxplot

Table 1. Four models that best fit the predation of loggerhead turtle hatchlings during their migration to the sea on Boa Vista Island, Cabo Verde. The models are ranked by lowest to highest Akaike's information criterion (AIC) values

Model	AIC	ΔAIC
Hatchling group size + distance to the sea + ghost crab hole density	550.67	0.00
Hatchling group size + distance to the sea × ghost crab hole density	552.28	1.60
Hatchling group size + ghost crab hole density	577.54	26.86
Hatchling group size + distance to the sea	600.93	50.26
Ghost crab hole density + distance to the sea	776.95	226.27
Distance to the sea × ghost crab hole density	778.74	228.06

predation rate of hatchlings estimated for the study beach was 29.4%. There was no significant relationship between the release distance from the sea and hatchling predation rate (Fig. 2c).

3.3. Effect of predator density

Ghost crab hole density influenced predation rate after controlling for group size ($F_{2,117}$ = 18.87, p < 0.0001). Post hoc analysis showed a significant difference between high and low densities of ghost crabs (p < 0.0001). In addition, we found significant differences between medium and low densities (p = 0.002), but not between high and medium densities (p = 0.375). Even at low ghost crab densities, predation rates were substantial (mean = 42.5%), but increased at medium (56.0%) and high densities (65.0%) (Fig. 2d).

4. DISCUSSION

Our study explored the effect of hatchling group size and ghost crab density on hatchling predation rates across various distances to the surf zone, in a major loggerhead turtle rookery at Boa Vista Island, Cabo Verde (Marco et al. 2012a). We also assessed the influence of time of day on predation rates. Our study provides valuable insights into trends in predation rates of ghost crabs that can inform best practice in conservation management of sea turtles during hatchling release. Specifically, we highlight the dramatic reduction in predation rates in daytime releases, and a lack of effect of the position of release on the beach.

The number of hatchlings we used in our experiments was within the range that occurs in natural emergence events, and similar to that recorded at other sea turtle nesting beaches (Drake & Spotila 2002, Glen et al. 2005, Adam et al. 2007). Although it is commonly assumed that all sea turtles emerge

from a nest more or less simultaneously, multiple emergence events from the same nest occur, with the number of hatchlings emerging at any of these events ranging from 1 to 120 (Glen et al. 2005). Such emergence patterns are similar among *in situ* and relocated clutches (Adam et al. 2007), and we therefore consider that our trials were as similar as possible to the conditions of a natural emergence.

Our results indicate that at João Barrosa beach, half (50.3%) of hatchlings die on their journey to the sea, almost solely due to ghost crab predation. Ghost crabs were the only predator observed on this beach, and a lack of other, large predators in Cabo Verde and a low human presence (at least on our study beach) may contribute to high ghost crab densities on this beach. The ghost crab predation rates of hatchlings we observed are similar to those reported by other studies, and indicate that ghost crabs are one of the main predators of sea turtle hatchlings during their crawl from the nest to the sea. For instance, ghost crabs preyed upon 24% of loggerhead hatchlings in Oslow Beach, North Carolina (Peterson et al. 2013) and contributed to 48% of total leatherback hatchling predation in Playa Grande, Costa Rica (Tomillo et al. 2010). In contrast, an overall predation rate of <4% was reported on olive ridley *Lepidochelys olivacea* hatchlings by ghost and hermit crabs in Playa Ostional, Costa Rica (Madden et al. 2008), and on the east coast of Florida, 7.6% of *Caretta caretta* hatchlings were preyed upon, with predators including mammals, birds and ghost crabs (Erb & Wyneken 2019). Such variation in mortality rates may be due to beach characteristics (morphology, vegetation cover), predator interactions, nesting seasons, hatchling size and the density and species of ghost crabs (Barton & Roth 2008). Beach characteristics may provide refugia and camouflage from predators, the abundance and densities of which may vary seasonally, whilst hatchling size may influence the vulnerability to predators by influencing locomotor performance (Booth 2017).

Sea turtle hatchlings generally emerge at night or at dusk, most likely to avoid risk of overheating and dehydration from daytime temperatures (Drake & Spotila 2002). This behaviour is therefore unlikely to be an anti-predator strategy (Gyuris 1994), and indeed, our results showed higher predation rates by ghost crabs during the night, lending further support to this idea. Whilst daytime emergence exposes hatchlings to higher predation by birds, predation by marine predators may be more likely (Gyuris 1994,

Whelan & Wyneken 2007), and nocturnal emergence may therefore allow hatchlings to enter the sea at a time of low visibility to aquatic predators (Gyuris 1994, Burger & Gochfeld 2014).

We found that predation rates differed between hatchling group sizes emerging from the nest, decreasing as group size increased, suggesting that synchronized emergence is an effective anti-predator behaviour (Glen et al. 2005, Marco et al. 2018b). In our study population, lower predation rates with greater group sizes may be a consequence of saturation of ghost crab foraging ability. A ghost crab that has captured a hatchling subsequently remains occupied consuming the hatchling for a few minutes, increasing the chance of other individual hatchlings in the same group escaping as suggested by Ischer et al. (2009). Furthermore, ghost crabs can only capture and handle 1 turtle hatchling at a time, which limits the number of individuals they can eat. Indeed, it was only in a very few events (6) that we observed ghost crabs capturing more than 1 turtle in a single release event, and this only occurred when the burrow was close to the nest. Such emergence strategies are fostered by natural selection acting as an evolutionary strategy to increase offspring survival (Glen et al. 2005). Predator saturation may not be the sole purpose of this behaviour, however, as synchronized digging in larger cohorts reduces the time and energy costs associated with escaping the nest (Rusli et al. 2016), allowing individual hatchlings more energy reserves for locomotor performance during crawling from the nest to the sea and off-shore swimming (Clusella Trullas et al. 2006).

High ghost crab densities were associated with higher loggerhead turtle hatchling predation. Predation levels at medium ghost crab densities, however, did not show a clear difference from low densities. In our study, ghost crab density was classified into 3 categories, where our high-density range (≥0.45 crab holes m^{-2}) was much wider than the low (0−0.18) and medium (0.19−0.40) densities. Considering such clear density-dependent processes on predation rates (Ischer et al. 2009), it is unsurprising that the effect would be negligible across predator densities of 0−0.18 or 0.19−0.40 crab holes m^{-2}. Furthermore, the similar predation rates at low and medium densities may be due, in part, to the difficulty of estimating ghost crab density with a precise method. We used the number of ghost crab burrow holes as a proxy for predator density, as the species' rapid movements make quantitative nocturnal counts particularly difficult. This method may yield much lower population estimates than occur in reality (Hobbs et al. 2008).

From a logical point of view, the greater the time spent on the beach, the higher the risk of hatchlings being preyed upon or becoming disoriented. However, in our study the predation rate did not increase with the distance to the sea. Furthermore, the highest predation rate (70%) observed in an individual trial occurred in the area between tide marks (distance 15 m). This is consistent with the observations made during our fieldwork and with previous studies on ghost crab behavioural patterns that indicate that burrow density is highest in the middle sections of a beach above the low water mark (Strachan et al. 1999, Türeli et al. 2009). Burrows of the largest crabs, and hence most likely the most effective predators, have also been recorded in these beach sections (Strachan et al. 1999, Türeli et al. 2009), possibly explaining the observed trend in predation rates. However, ghost crab predation of nests located near dunes on Boa Vista Island has also been observed (Marco et al. 2015), suggesting that the presence and abundance of sea turtle nests far from the shoreline may have led to an expanded ghost crab feeding habitat.

Our results can help inform best practice guidelines for the release of hatchlings at sea turtle nesting beaches where ghost crab predation of hatchlings is abundant. In hatchery management programmes at such beaches, we recommend release of hatchlings in large groups, in areas of low ghost crab density where possible, and suggest that the release personnel remain vigilant until hatchlings reach the sea. This is especially relevant in the areas just above the wave wash zone, where ghost crab predation of sea turtle hatchlings is greatest. Conservation programmes may even go so far as to remove or at least disturb ghost crabs from an area during hatchling release. Although the mortality rate due to predation was at its lowest during the day, it is known that hatchlings can die from other causes (dehydration and disorientation). Release during the day is thus not recommended and twilight releases are preferable to reduce predation risk. Furthermore, releasing hatchlings in areas near structures that may act as fish aggregation devices such as reefs or jetties should be avoided to reduce the presence of marine predators (e.g. Wilson et al. 2019).

Finally, at João Barrosa beach, whilst predation rates decreased with decreasing ghost crab density (Fig. 2d), it is important to highlight that even at low ghost crab densities, the predation rate (42.5%) was still significant. We recommend that future studies investigate the ghost crab density at other sea turtle nesting beaches to identify the risk of hatchling mor-

tality, and to determine whether management strategies that mitigate ghost crab predation should be considered.

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