Hawksbill (*Eretmochelys imbricata*) and Green Turtle (*Chelonia mydas*) Nesting and Beach Selection at Príncipe Island, West Africa

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Hawksbills (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) are the predominant nesting sea turtle species on the beaches of Príncipe Island in the Gulf of Guinea. The extent of nesting has been largely unknown, but such information is essential for management and conservation. Our study is the first island-wide nesting assessment. Results from the survey, conducted from 1 December 2009 to 18 January 2010 (during peak nesting season), show that the potential suitable nesting area (10 km) is scattered around the island's 50 beaches. Sea turtles nested on 32 of the beaches (hawksbills, 20; green turtles, 28) and used 7.5 km of the suitable nesting habitat (hawksbills, 5.8 km; green turtles, 7.0 km). We estimated that 101 (95% CI = 86–118) clutches were deposited by 17-29 hawksbills and 1088 (95% CI = 999–1245) clutches were deposited by 166-429 green turtles on Príncipe from November 2009 to February 2010 (nesting season). Long-term green turtle nest count data collected from 2007/08 to 2015/16 suggest a positive trend. Analyses of clutch densities in relation to beach characteristics suggested that both species preferred areas where human presence is lower, which coincided with the most sheltered areas. These findings should be used to inform coastal planning and minimize impacts on nesting beaches, as Príncipe is currently targeted for tourism development. Overall, results highlight that Príncipe beaches are very important for the conservation of West African hawksbill and green turtle populations.

Key words: assessment, Gulf of Guinea, population, reproduction, sea turtle

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INTRODUCTION

Príncipe, the smaller island of the São Tomé and Príncipe Republic, located in the Gulf of Guinea, has recently been designated as a UNESCO Biosphere Reserve (2012). The Gulf of Guinea harbours major nesting aggregations of hawksbill (*Eretmochelys imbricata*) and leatherback (*Dermochelys coriacea*) turtles as well as regionally important populations of green turtles (*Chelonia mydas*) and olive ridleys (*Lepidochelys olivacea*) (Fretey 2001; Formia et al. 2006; Mortimer and Donnelly 2008; Tomás et al. 2010; Metcalfe et al. 2015). However, leatherbacks and olive ridleys rarely nest on Príncipe; here the beaches are mainly used by the critically endangered hawksbill and by the endangered green turtle (Fretey 2001; http://www.iucnredlist.org/).

Both adult hawksbills and green turtles migrate from foraging to nesting grounds, sometimes thousands of kilometers, to lay several clutches of more than 100 eggs in or near the area where they hatched (philopatry), making most nesting colonies different in regard to population genetic structure (Miller 1997; Bowen & Karl 2007; Hays & Scott 2013). Recent stable isotope analyses suggested that most of Príncipe's breeding female hawksbills forage close to the nesting grounds, on the insular platform (Ferreira et al. 2018), while green turtle foraging grounds may cover a much larger area, chiefly in the Gulf of Guinea (RLF, unpubl. data). The longer migration of the green turtles requires accumulation of large energy reserves, meaning that this reproductive migration is dependent on environmental conditions at foraging grounds. The herbivorous green turtle is typically affected more by this variation than the carnivorous marine turtle species, and, consequently, nesting numbers vary substantially from year to year (Broderick et al. 2001; Solow et al. 2002).

Quantifying nest numbers allows an estimation of population size and trends, which are crucial information for science, conservation, and management (Gerrodette & Taylor 1999; Girondot 2010). These data can be readily obtained from nesting surveys, representing a standardized and repeatable record of nesting activity to assess and monitor population status (Gerrodette & Taylor 1999; Schroeder & Murphy 1999; National Research Council 2010). Nesting surveys are based on the fact that each time a female turtle emerges from the water to deposit a clutch, she leaves a set of tracks in the sand (e.g. body pit) that can be used to infer the number of nests (i.e., clutches) on the beach (Schroeder & Murphy 1999; National Research Council 2010). When nesting occurs on a large number of small and dispersed beaches, reliable nest estimates can be attained with two to three weeks of monitoring during peak nesting of a fraction of the available beaches (Eckert 1999; Jackson et al. 2008; Girondot 2010; Delcroix et al. 2013). Although several sea turtle projects have been carried out in São Tomé and Príncipe during the past 20 years, they have focused on a small fraction of the islands' beaches, and information on the extent of nesting and available habitat is incomplete.

Nesting surveys, in addition to being useful in studying reproduction and nest biology (Miller 1997), can provide information about beach selection. The locations where females emerge to nest have consequences for their survival and that of their offspring (Mortimer 1982; Bjorndal & Bolten 1992). The small island of Príncipe, where a large number of different types of beaches occurs, is an ideal place to conduct an analysis of beach selection.

Although no accurate information on population sizes and status exists for the São Tomé and Príncipe rookeries, hawksbill nesting in the country is considered to be the most important in the Eastern Atlantic and is the top priority for the conservation of the species in the region (Fretey 2001: Mortimer & Donnelly 2008). The eastern Atlantic hawksbill population was ranked as one of the 11 most endangered sea turtle Regional Management Units in the world (Wallace et al. 2011), highlighting the importance of nesting surveys in São Tomé and Príncipe. Green turtle nesting, however, has historically been lower than other regions of the East Atlantic (e.g., Bioko, Poilão and Ascension islands), but breeding females exhibit a relatively higher mitochondrial diversity in São Tomé and Príncipe (Formia et al. 2006).

In the present study, we identify and describe sea turtle nesting along the entire coast of the island of Príncipe to aid sea turtle conservation and the sustainable development of the island's littoral habitat. We estimated the numbers of clutches based on one-time body-pit counts per beach and regular monitoring of a fraction of those beaches during peak nesting season, complemented with clutch data from the intensively monitored Paciência beach. Our method was simple and provided information on the nesting abundance and distribution throughout Príncipe Island, as well as an estimation of the breeding female numbers. We also investigated possible patterns of beach selection by nesting females by comparing clutch densities with recorded beach characteristics.

MATERIAL AND METHODS

Study Site

The island of Príncipe (140 km^2; 1º37'N; 7º23'E) is located 220 km west of the African continent, 145 km northeast of São Tomé and 205 km southwest of Bioko (Fig. 1). The warm and humid equatorial climate supports dense vegetation. Although it rains year-round, there are two drier seasons: one from June to September (Gravana) and another from mid-December to early-February (Gravanita). The second drier season is characterized by higher temperatures and lower precipitation levels and largely overlaps with the reported sea turtle nesting season, from November to January (Graff 1996). Permanent fishing communities, and most of Príncipe's 7500 human inhabitants (National Institute of Statistics 2013), are located in the sheltered and less mountainous northern half of this deeply eroded and ancient volcanic island (ca. 30 Ma; Dunlop & Fitter 1979). Currently, only two small, isolated fishing communities exist in the south, which are mostly accessed during fishing campaigns.

Fig. 1. Location of islands in the Gulf of Guinea relative to the African coast.

Data Collection

Beach surveys were undertaken during the peak of the 2009-2010 nesting season, from 1 December 2009 to 18 January 2010. The entire shoreline of Príncipe (ca. 100 km) was surveyed primarily on foot, although boats and/or motorcycles were used occasionally. Nesting activity was quantified by one-time body-pit counts on each beach. More frequent, systematic crawlcounts on all the beaches were not feasible due to the island geography and financial constraints (e.g., boat rental). Species were distinguished based on their track morphology and nest location (Pritchard & Mortimer 1999). In addition to the one-time survey of the entire island, nine body-pit count surveys, distributed over the 49 days, were conducted on two nesting beaches in Infante Bay (Fig. 2, beaches 14 and 15) to develop accumulation curves of body pits for each species throughout the season. Finally, sporadic night patrols were conducted on the two Infante Bay beaches and on three other beaches (Rio São Tomé, Rio Porco, and Praia Seca) to estimate the ratio of body pits to clutches for each species. This ratio is essential to convert body-pit counts to clutch counts because a female may dig a body pit without depositing a clutch of eggs.

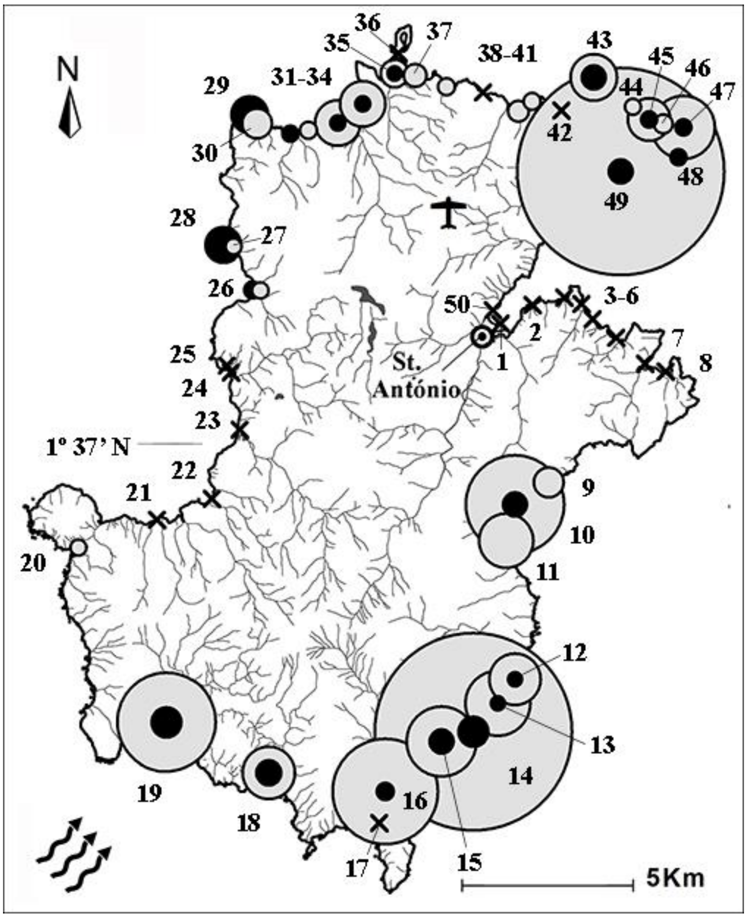

Fig. 2. The island of Príncipe with estimated clutch abundance proportions for the beaches in the 2009/2010 nesting season. Filled circles represent number of clutches, from 2 to 315, black for hawksbills and grey for green turtles. X's indicate beaches without observed turtle activities and arrows indicate prevailing winds and currents. Human population is concentrated north of latitude 1° 37' N. City of Santo António, airport and beach numbers (see Appendix for names) are also illustrated.

Longitudinal beach lengths at the high tide line were recorded with a global positioning system (GPS) unit. The length of suitable nesting habitat (i.e., no obstacles and enough sand to allow digging of a nest cavity) was determined in addition to total beach length. Also, information was collected on beach characteristics that might affect nesting (see Beach Selection Analysis section, below).

Abundance Analysis

To convert our body-pit counts on a single day (n) for each beach to estimates of the total number of clutches for each species deposited on each beach in the 2009/2010 study period, we need three conversion factors. First, we need the proportion of total body pits for the year created for each survey day (n) or daily cumulative value $dc(n)$. These proportions were generated by regressing cumulative body-pit proportions from the nine body-pit surveys on the two Infante beaches against date and using this regression to generate the proportion of body-pits created by each date. The cumulative proportions from the Infante beaches for both hawksbills and green turtles were assumed to be representative for all beaches.

Second, we need to estimate the proportion of body pits that have been obscured before the survey day by spring tides, wave splashes, and heavy rainfalls, which affect the persistence of body-pits on the beach (Schroeder & Murphy 1999). We used a correction factor (cf) based on the survey day (n from 1 to 49). At every spring tide, we assumed that half of the body-pits were wiped out by the sea or rain (RLF, pers. obs.): $cf(n) = 1$, if $n \leq 16$; 1.5, if $16 < n \leq 30$; 2, if $30 < n \leq 45$; and 2.5, if $n > 45$.

Third, we need the ratio of clutches to body-pits to convert the total number of body pits per beach to the number of clutches per beach. We calculated this ratio based on sporadic night patrols conducted on the two Infante Bay beaches and on three other beaches (Rio São Tomé, Rio Porco, and Praia Seca) and on observed number of clutches laid on the intensively monitored Paciência beach (reported by the local monitoring program) and the expected number of body-pits for Paciência beach during the study period. The clutch to body-pit ratio was assumed to be similar among beaches, except for Rio São Tomé beach where discrepancies for green turtles were observed and corrected.

As a result, the expected number of body-pits (ep_x) for each beach (x) for the study period was obtained as follows:

$$ep_x = [op_x(n) + (op_x(n) \text{ x } cf(n))] / dc(n) \qquad \text{Eqn. 1}$$

where $op_x(n)$ = the observed number of body-pits for beach x on day n, $cf(n)$ = the correction factor for proportion of nests obscured by day n, and $dc(n)$ = the proportion of body pits created by day n.

The number of clutches were estimated for each beach (nc_x) with the following formula:

$$nc_x = ep_x \times cbp \qquad \text{Eqn. 2}$$

where ep_x = expected number of body-pits for a beach and cbp is the clutch to body pit ratio for the entire nesting season (1 September 2009 to 28 February 2010) from Paciência beach (observed clutch number / expected body pit number). We incorporated uncertainty by imposing an error level to each estimated model input, resulting in a range of values with 95% level of confidence (i.e., 95% CI). While the regression coefficient ($1\text{-} R^2$) was used for $dc(n)$, which differs between species, a 5% error was assigned to $cf(n)$ and to the quotient between observed clutches and estimated body pits on Paciência beach.

An indirect method to estimate the annual number of nesting females can be derived from dividing the total number of clutches by the clutch frequency, defined as the average number of nests laid per female during a season (Alvarado & Murphy 1999). Since estimates of Príncipe sea turtles were not available, the values used were obtained from the literature: 4–5 nests per season for hawksbills nesting at Seychelles (Indian Ocean) and Antigua (Caribbean) islands (Mortimer & Bresson 1999; Richardson et al. 1999); and 2.9–3.1 for green turtles nesting at Alagadi (Mediterranean) and Bioko (Gulf of Guinea) islands (Broderick et al. 2002; Tomás et al. 2010). However, for green turtles, a value of six was used as the maximum because recent tracking studies had shown that clutch frequency might be underestimated in some populations (Weber et al. 2013; Esteban et al. 2017).

Beach Selection Analysis

Because clutch abundances are expected to be positively correlated with beach size (Mortimer 1982), densities (clutches/km of suitable sections of beach) were used to explore the nesting distribution in relation to the recorded beach characteristics. Beaches with a large amount of obstacles that impeded nesting (e.g., organic and artificial debris, armoring) were not included in the analyses. The observations were grouped in four categories (Table 1) from each of the seven recorded qualitative and quantitative

Table 1. Recorded qualitative and quantitative beach characteristics, that might affect sea turtle nesting on Príncipe, and the criteria and conditions used for their classification into four categories (1–4).

Characteristic	Description	Obtained	1	2	3	4	Condition
Total length	longitudinal size (m) of the beach	*in situ* with a GPS	≤100	>100; ≤300	>300; ≤600	>600	-
Suitable length	longitudinal distances (m) with minimal nesting conditions	*in situ* with a GPS	≤75	>75; ≤225	>225; ≤450	>450	-
Sand color	subjective rating, from lighter to darker	*in situ*	yellow	light brown	brown	dark brown	-
Grain size	subjective rating, partially based on the Wentworth (1922) scale	*in situ*	very fine	fine	medium	coarse	-
Slope	distance (m) from the middle of the beach to the 10 m isobath	nautical chart	>900	>600; ≤900	>300; ≤600	≤300	-
Exposure	beachfront orientation relative to the prevailing wind and current	nautical chart and *in situ*	-	NE	NW and SE	SW	minus 1 if protected by the shoreline
Threat	minimal distance (m) from the beach to the nearest settlement	nautical chart and *in situ*	>1000	>500; ≤1000	≤ 500	-	plus 1 if located north of 1º37'N

characteristics of the beach (i.e., total and suitable lengths, sand color and size, slope, exposure and threat), allowing the use of continuous statistical methods (Bentler & Chou 1987; Mason 1994). Chi-square tests were used to evaluate whether the numbers of beaches in each category for each characteristic were similar and whether the distributions of clutch abundance and density among beaches, for both species, were different from those expected by chance. Because all data were not normally distributed, non-parametric Spearmen R correlations were used to explore the relationships between all pairs of variables. Multiple regression was also employed to suggest which beach characteristics might have a major effect on clutch densities. Statistical significance was assessed using Statistica software (StatSoft, Inc.) with an alpha of 0.05.

RESULTS

Eighty beaches were identified along the 100 km coastline of Príncipe Island. Fifty beaches had a total of 10 km shoreline with suitable morphological conditions to support nesting (mean ± SD (range) = 200 ± 223.1 m (9–1255 m), n = 50), and 17.8 km of total beach length (356 ± 295.6 m (62–1500 m), n = 50) (Appendix). In general, beaches were predominantly backed by coconut plantations, although lowland rain forest and scarps also occur. The nesting area under the over-story vegetation was characterized by the presence of more compact sand with higher organic matter and a small degree of low-lying vegetation. Beaches appeared to be homogeneous in widths and in the proportion of sunny to shaded areas. All had several permanent streams or rivers but erosion by heavy rains or river flooding is not common. Approachability from the sea was also similar among beaches, except on Ponta Pedra Furada and Ponta Marmita, where green turtles could not emerge due to a rocky foreshore.

Abundances

Sea turtle nesting was observed on 32 of the 50 suitable nesting beaches, 20 for hawksbills and 28 for green turtles (Fig. 2, Appendix). The best fit to the cumulative body-pit frequencies, observed in the two Infante beaches, was a nearly linear second degree equation, for both hawksbills (total number of body pits = 16; $R^2 = 0.94$; *cumulative body pits* $= 0.004n^2 + 0.014n + 5.157$) and green turtles (total number of body pits = 389; $R^2 = 0.99$; *cumulative body pits* $= 0.075n^2 + 3.651n + 29.694$). Clutch abundances for each beach (nests/beach) for the entire nesting season, estimated using equations 1 and 2, and using 6 hawksbill and 315 green turtle clutches reported for Paciência beach during the entire nesting season in 2009/2010 (H. Carvalho, pers. comm.; Loureiro et al. 2011), ranged from 2 to 12 hawksbill turtle clutches (mean = 5 ± 3.2 (SD), n = 20) and from 2 to 315 green turtle clutches (38.8 ± 77.5, n = 28) (Fig. 2, Appendix).

Although clutch to body-pit ratios appeared similar among beaches, in Rio São Tomé beach a large amount of cut coconut palm logs blocked suitable green turtle nesting area, increasing the ratio by 30% (7:2), in comparison to the ratio (32:13) observed on the other beaches during night patrols. This resulted in an estimate of 101 hawksbill (95% CI = 86–118) and 1088 green turtle (95% CI = 999–1245) clutches laid during the 2009/2010 nesting season. Applying the range of clutch frequencies from the literature to the total clutch counts, approximately 17–29 (95% CI) female hawksbills and 166–429 (95% CI) female green turtles used the island during the 2009/10 nesting season.

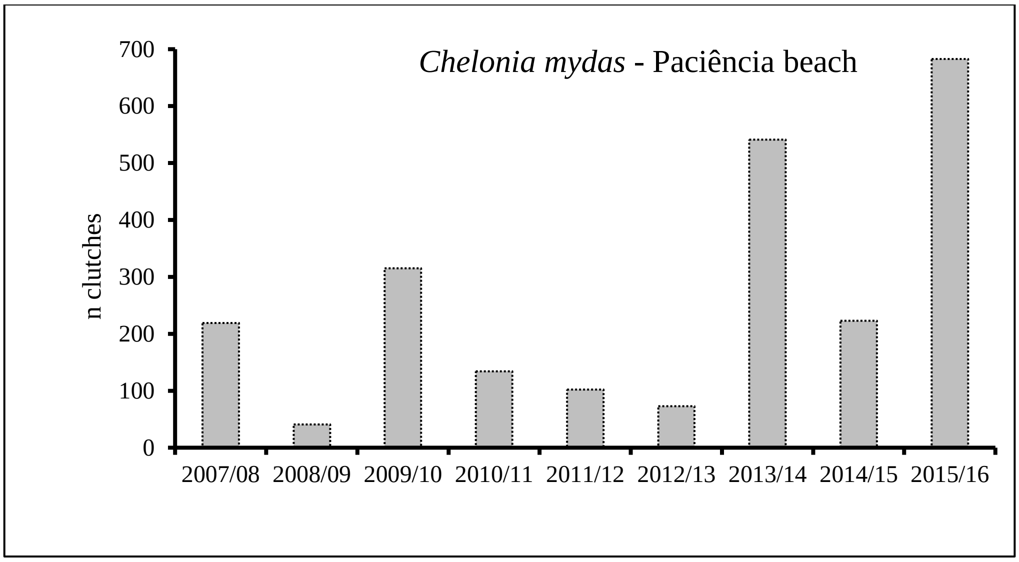

Fig. 3. Total number of green turtle clutches laid at Paciência beach, Príncipe Island, from 2007/08 to 2015/16 nesting seasons.

Long-term clutch data were available for green turtles for 9 consecutive seasons from Paciência beach: 2007/08, 219 clutches (Z. Rodriguez, pers. comm.); 2008/09, 41 (E. Neto, pers. comm.); 2009/10, 315 (Loureiro et al. 2011); 2010/2011, 134; 2011/12, 102; 2012/13, 73; 2013/14, 541; 2014/15, 223; 2015/2016, 683 (H. Carvalho, pers. comm.). These data (9 seasons) suggest a positive trend of the nesting population (Fig. 3).

Although estimated clutch numbers were significantly different among beaches for both species (all *P*'s < 0.001, df = 49), hawksbill abundances were not as clumped as observed for green turtles (Fig. 2). However, two northwest situated beaches, Ponta Marmita and Ponta Pedra Furada, accounted for almost a quarter (23.5%) of the hawksbill nests. These two beaches possessed sharp rocks on the foreshore, and no green turtle body-pits or tracks were observed there. Two green turtle nesting beaches accounted for more than half (55.4%) of clutches: Paciência in the northeast (315 clutches, observed) and the larger of the Infante beaches in the southeast (288 clutches, 95% CI = 257–321). If the two beaches located in Infante Bay are combined, as represented on maps, then 324 (95% CI = 290–361) green turtle clutches were laid there. Although the great majority of the potential nesting beaches (72.5%) and suitable nesting habitat (78.5%) are located in the North (> latitude 1º37'N), more than half of the total number of clutches were laid in the South (58.6%) (hawksbills, 43.7%; green turtles, 59.9%). Also, 79% of the green turtle clutches were laid on only 6 beaches, 5 of them located to the south of the island.

Beach Selection

Clutch densities (nests/km) by beach, for both species, also differed significantly among beaches (all P's < 0.001, df = 49) and were not normally distributed. Estimated hawksbill nest densities ranged from 4.8 to 150.7 (mean ± SD 38.8 ± 47.3, n = 20), within 5.8 km of suitable habitat. For green turtles, they ranged from 6.8 to 564.9 (mean ± SD 151.2 ± 164.2, n = 28), on 7 km of suitable habitat (see Appendix). The beach with the combined highest density of sea turtle nesting was Infante (582.2 clutches/km), which ranked second in abundance. Paciência, the longest beach with the highest abundance, ranked eighth in nest density (255.8 clutches/km). The seven beaches with nest density higher than that of Paciência were all located in the south, accounting for almost half (49.4%) of the total number of clutches laid in Príncipe.

Recorded beach characteristics (i.e., total length, suitable length, sand color, grain size, slope, exposure and threat) were not normally distributed and, except for suitable length (P < 0.104, df = 3) and almost for sand color (P < 0.016, df = 3), differed significantly among beaches (all P's < 0.002, df = 3). Two beaches, Candeia and Bom-bom, had large amounts of obstacles on the beach (e.g., organic and artificial debris, armoring), which impeded sea turtle nesting, and these were removed from the analysis for both species. In one of them (Candeia), we observed a hawksbill track with no body pit below high tide line, but no body-pits or tracks were found (confirmed by other visits later in the season). For green turtles only, two beaches with sharp rocks on the foreshore that prevented this species from nesting were removed from the analyses (Ponta Pedra Furada and Ponta Marmita). While hawksbill and green turtle densities were correlated with one another (r_s = 0.60, P < 0.001, n = 46), also with excluded beaches (r_s = 0.47, P < 0.001, n = 50), both were significantly correlated with exposure and threat (Table 2). In addition, exposure was correlated with threat, suitable length with total length, and slope with grain size and exposure (Table 2).

From the multiple regressions, although the overall relationship of beach characteristics with hawksbill clutch densities was significant, the fit was poor and only the effects of exposure and total length were significant. For green clutch densities, the fit was a little better, the relationship was significant, and the effect of threat was the only significant parameter (Table 3).

Table 2. Spearman R correlations (r_s) between densities (clutches/km) and beach characteristics (1–4) recorded at Príncipe, for both species. Only significant results are presented (all P*'s* < 0.01).

Variable	n	Total length	Grain size	Exposure	Threat
Density					
Hawksbill	48			0.45	-0.43
Green turtle	46			0.44	-0.62
Beach characteristic					
Suitable length		0.76			
Slope	50		0.41	0.39	
Exposure					-0.52

Table 3. Multiple regression output between clutch densities (clutches/km) and beach characteristics (1–4), for hawksbill and green turtle nesting at Príncipe. Predictors with significant effects are also presented.

	n	Statistic	R^2_{adj}	*P*	SE	Predictor
Hawksbill	48	$F_{7.40} = 3.77$	0.31	0.003	30.1	Exposure: $t_{40} = 2.51$; $P = 0.016$ Total length: $t_{40} = -2.28$; $P = 0.028$
Green turtle	46	$F_{7.38} = 6.41$	0.46	<0.001	104.6	Threat: $t_{38} = -4.81$, $P < 0.001$

DISCUSSION

Sea turtle nesting is scattered around Príncipe Island, with reduced frequency on the more exposed and rockier west coast and in sites with high human population densities. On two beaches with the highest abundance of hawksbill clutches, Ponta Marmita and Ponta Pedra Furada in the northwest (25% of total), green turtles did not emerge due to a dangerous rocky foreshore. Two beaches, Paciência in the northeast and Infante in the southeast, hosted 55% of the green turtle clutches. These observations overlapped with earlier observations of Castroviejo et al. (1994) and Juste (1994), who listed Infante and Paciência beaches, among others, as the most important for sea turtle nesting in Príncipe. Our results expand upon the conclusions of more recent studies. Monzón-Argüello et al. (2011) indicated that the main hawksbill nesting beaches are located on the northern, eastern, and southern coasts of the island, while Loureiro et al. (2011), who only monitored northern beaches, reported Paciência as the most visited beach by nesting green turtles.

Abundances

Although there is uncertainty in our model, the estimated annual number of hawksbill clutches for Príncipe Island (86–118 clutches) was much higher than that of any other West African location where nesting has been reported (Mortimer & Donnelly 2008). For example, at the neighbouring Bioko Island, only 22 hawksbill clutches were reported during two nesting seasons, 1996 and 1998 (Tomás et al. 2010). Although there are no estimates for the entire island of São Tomé, almost 130 hawksbill nests were recorded on the monitored beaches during the recent 2016/17 nesting season (S. Vieira, pers. comm.). Thus, it is likely that hawksbill nesting in Príncipe ranks among the highest in the region. Estimated clutch abundance translates to 17–29 hawksbills nesting at Príncipe in the 2009/10 nesting season. This estimate may be biased low, as hawksbills leave little or no body-pits in the littoral forest (Pritchard & Mortimer 1999), and our estimated annual abundance is 50% of that previously assumed (<50 females/year; N. Loureiro, pers. comm. *in* Monzón-Argüello et al. 2011). Nonetheless, our annual nesting hawksbill estimate represents a large proportion of the total annual numbers of nesting females expected for the entire West African region (100 females/year; Mortimer & Donnelly 2008). An estimated 100–150 adult hawksbills were captured annually in Príncipe in the early 1990's (Castroviejo et al. 1994; Juste 1994). Although these figures include captures at sea and males, based on informal interviews with older inhabitants, sea turtle capture was on a small-scale prior to independence in 1975, in part because of the availability of other sources of meat. The danger of losing important hawksbill genetic diversity is a reality, particularly because the high value of hawksbill scutes for craftwork makes them a highly valued target (Ferreira 2015), and other anthropogenic activities threaten every life stage of sea turtles (e.g., bycatch and coastal development; Donlan et al. 2010). Based on an 11-year study with hawksbills from Antigua Island, Richardson et al. (1999) calculated that one adult female hawksbill must breed for at least 4.1 nesting seasons to replace herself, and some of them must be reproductively active for decades to compensate for the early mortality of others. Emerging from the sea several times during the season makes sea turtles very vulnerable to exploitation, but once effective protection is provided, the increase in nesting activity can be dramatic (Mortimer & Bresson 1999), even at sites with low abundance (Mazaris et al. 2017).

Although inter-annual variation in nesting numbers is very high for green turtles (Broderick et al. 2001), the green turtle clutch estimate for Príncipe (999–1245 clutches, 2009/10 season) fall within the range reported on the neighboring island of Bioko (1255–1681 clutches, 1996/97-1997/98 seasons, Tomás et al. 2010; ca. 180 to 3900 clutches, 2000/01 to 2013/14 seasons, Honarvar et al. 2016). However, the extent of the nesting habitat used in Bioko (19.3 km; Tomás et al. 2010) was much greater than in Príncipe (7.5 km). All these clutch estimates are small relative to those reported from Ascension and Poilão, islands located outside of the Gulf of Guinea (Catry et al. 2009; Weber et al. 2014). Although the Ascension population is still recovering (Weber et al. 2014), Poilão might be reaching the limit of nesting supported by the available habitat, where 7000–29000 clutches are laid annually in only 2.3 km of beaches (Catry et al. 2009). If protection of nesting females and their eggs is achieved, as occurs on Ascension and Poilão (Catry et al. 2009; Weber et al. 2014), the islands in the Gulf of Guinea could stand out significantly since more nesting habitat will be available. Although the present estimate of 166–429 nesting green turtle females for Príncipe in 2009/10 more than double previous population estimates (75–100/year; Formia et al. 2006), it continues to be low. Low nesting has also been documented elsewhere in the Gulf of Guinea (e.g., 63–649 nesting females/year at Bioko; Honarvar et al. 2016), and our results reinforce the urgency to study and conserve all life stages. Even so, it is possible that the positive trend observed at Príncipe is connected to the recent great decrease in female capture following the approval of the regional sea turtle protection law in Príncipe (Regional Legislative Decree 2009). Positive trends in sea turtle populations are likely to be associated with the protection of nesting females and their eggs (Mazaris et al. 2017). Since Príncipe has a small human population (7500 inhabitants; National Institute of Statistics 2013), full protection could be achieved if resources are used effectively, transforming the island into a safe habitat for sea turtles to buffer against their extirpation in the region.

Beach Selection

Although nesting habitats were scattered around Príncipe Island, clutch densities were not distributed evenly. Nesting densities and abundances were generally higher in southern beaches, within the Natural Park limits (see Albuquerque & Cesarini 2009), suggesting that the human population, which is highly concentrated in the north, may impact distribution. While both exposure and threat were correlated with hawksbill and green turtle clutch densities, although in opposite directions, they were also negatively correlated with each other. Considering that human settlements occupy the most sheltered areas, the effect of both threat and exposure is expected. However, for hawksbills, the multiple regression did not show threat as most relevant, as it did for green turtles, but rather exposure and the inverse influence of total beach length. We believe these results might be a consequence of the two most important hawksbill beaches being very small, exposed, and situated in small rocky peninsulas on the north inhabited area, that are not easily accessed by people. Therefore, the risk of poaching might be smaller than expected. In addition, hawksbills are smaller than green turtles and dig much more shallow body pits, allowing hawksbills to emerge, lay their eggs, and return to sea much faster, sometimes during the day (Miller 1997; Ferreira & Martins 2013). Exposure, besides being correlated with threat, was also correlated with beach slope. In turn, slope was also correlated with grain size, which is typically larger on higher slope beaches and on beaches exposed to high-energy waves (Komar 1976). Hawksbills may prefer high-slope beaches, that provide females and hatchlings with reduced travel distances, costs, and predation risk (Horrocks & Scott 1991).

Although hatching success is influenced by sand characteristics (Ackerman 1997; Miller 1997), sea turtles nested in all types of sand on Príncipe. The same was reported for Ascension Island, where biotic factors like predation and competition may be more relevant than the characteristics of the sand or other geologic factors (e.g., offshore approach, obstacles; Mortimer

1982). This supports the hypothesis that it might be better for females to select a nest site based on their survival rather than on the survival of their eggs (Bjorndal & Bolten 1992). Although habitat availability is a relevant factor, results from this study suggest that green turtle nest densities are higher on beaches with lower threat, that is, farther away from human settlements. This may be driven by differences in mortality between beaches or also by turtles actively avoiding the riskier areas, as sea turtles do in foraging habitats to avoid predators (Heithaus 2013). Further evidence indicates that green turtles nesting on the isolated Infante beaches have larger body sizes than in Paciência beach (RLF, unpubl. data), where threats are higher. This could be related to smaller females, likely younger and less experienced, preferring Paciência beach due to better nesting conditions (space and approachability). Weber et al. (2014) also found an inverse relationship between nesting intensity and distance to the main human settlement for green turtle nesting at Ascension, which may reflect an increase in nesting due to effective protection and conservation measures after severe exploitation. This suggests that if harvests of females and eggs decrease at Príncipe, and other threats on the beach (e.g., construction and denaturalization) do not increase, nesting on the northern beaches has the potential to surpass that on southern beaches because more habitat is available.

Conservation Insights

The approbation of the local sea turtle protection law (Regional Legislative Decree 2009) is the result of a committed regional government wanting to develop the island in harmony with the local biodiversity and culture, despite the constraints of being a small, poor and isolated island where people are highly dependent on their natural resources to subsist. Those actions pass through attracting and supporting tourism investors, in preference to less environmentally friendly activities like extensive palm oil plantations or hydrocarbon extraction infrastructures. Recently, another seaside resort became operational (in Sundi beach), where the fishing community was relocated to areas around the city bay. Besides the impacts on local people lives, coastal development has recognizable negative impacts on sea turtles that should be prevented or mitigated (e.g., beach armoring, lighting). In addition, a common negative practice observed is the removal of organic matter and low-lying vegetation on beaches and their backshores. This practice compacts the sand under the over-story vegetation (mostly coconuts) and may cause that nesting habitat, mainly used by hawksbills, to become unsuitable or decrease thermal variation and impact sex-ratios, limiting the resilience to changes in global temperatures (Kamel 2013). In a recent visit to the island (January 2017), RLF observed the tracks from a hawksbill unsuccessful emergence that went through a large extension of Banana beach backshore, a beach that just started to be controlled by a resort (e.g., diving center, bar, esplanades). Thanks to the positive results of the protection and awareness initiatives following legislation, a plan to construct a hatchery near another tourist resort (Bom-bom) was abandoned, thus reducing further negative impacts on incubation conditions (Mortimer 1999; Mrosovsky 2006). Another emerging trend is cement-based construction being encouraged instead of traditional wooden houses, which leads to sand extraction on the beaches and consequent negative impact on tourism and sea turtles. Noteworthy, the increase in dampness and mold in cement homes might also have negative consequences on human health (Krieger 2010), that may lead to an increase in the demand for the local traditional medicine to cure asthma, made from dried sea turtle penis.

CONCLUSIONS

Our main goal was to identify the extent of the nesting habitat and provide an island-wide estimate of clutch numbers – indispensable information for assessment of population status and trends (Schroeder & Murphy 1999; Girondot 2010). This study demonstrated that Príncipe represents a significant nesting area for hawksbills in the Eastern Atlantic, although nesting in other potentially important areas should be assessed (e.g., São Tomé, where more nesting habitat is available). The small size of hawksbill and green turtle nesting stocks in the Gulf of Guinea suggests that the illegal take of females at São Tomé and Príncipe (Ferreira 2015), both on the beaches and at sea, is a serious threat for these sea turtle populations. Fortunately, recent sea turtle conservation efforts involving turtle fishers and turtle traders show very positive signs (Vieira et al. 2017a,b) and highlight the importance of integrating local people that used to make a living with sea turtles (Frazier 1999; Ferreira 2015). The relative nest abundances observed among the beaches, and their association with human distribution, can now aid managers and conservationists to adopt more informed and efficient measures (e.g., in coastal development planning and sea turtle monitoring). Our approach can also be used for future population assessments, especially if the robustness of the method is increased by: (1) replicating the method to obtain variances or year to year deviations; (2) evaluating clutch to body-pit ratio variation between beaches or beach types; (3) reducing the number of days between beach counts and increase the total numbers of counts; (4) obtaining accurate body-pit persistence time for different beach types; (5) regularly monitoring main beaches during the nesting season; and (6) obtaining more precise data on clutch frequency and remigration intervals. Since hawksbill nesting was more dispersed than that of green turtles, periodic monitoring of several beaches will be necessary to assess population status. On the other hand, the assessment of green turtle population size and trends can be efficiently conducted by integrating the monitoring and protection of the two main beaches (Paciência and Infante), increasing efficiency and allowing for funds to be invested in other essential activities. We recommend the adaptation of this method to other regions where low-density nesting is also scattered across numerous small, interspersed beaches and where financial resources are limited.

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REFERENCES

Ackerman, R.A. 1996. The Nest Environment and the Embryonic Development of Sea Turtles. Pp. 83–106 in: The Biology of Sea Turtles, Vol. I. Lutz, P.L.and J.A. Musick (Eds). CRC Marine Science Series, CRC Press, Inc.446pp.

Albuquerque, C. and D. Cesarini 2009. Plano de Manejo do Parque Natural do Príncipe, 2009/2014. 146 pp.

Alvarado, J. and T.M. Murphy 1999. Nesting Periodicity and Internesting Behavior. Pp. 115–119 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K., K. Bjorndal, F. Abreu-Grobois, and M. Donnelly (Eds). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Bentler, P.M.and C.-P.P. Chou 1987. Practical issues in structural modeling. *Sociological Methods and Research* 16:78–117.

Bjorndal, K.A. and A.B. Bolten 1992. Spatial Distribution of Green Turtle (*Chelonia mydas*) Nests at Tortuguero, Costa Rica. *Copeia* 1992:45–53.

Bowen, B.W.and S.A. Karl 2007. Population genetics and phylogeography of sea turtles. *Molecular Ecology* 16:4886–4907.

Broderick, A.C., F. Glen, B.J. Godley and G.C. Hays 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* 36:227–235.

Broderick, A.C., B.J. Godley and G.C. Hays 2001. Trophic status drives interannual variability in nesting numbers of marine turtles. Proceedings of the Royal Society, Biological Sciences 268:1481–1487.

Castroviejo, J., J. Juste, J.P. del Val, R. Castelo and R. Gil 1994. Diversity and status of sea turtle species in the Gulf of Guinea islands. *Biodiversity and Conservation* 3:828–836.

Catry, P., C. Barbosa, B. Paris, B. Indjai, A. Almeida, B. Limoges, C. Silva and H. Pereira 2009. Status, Ecology, and Conservation of Sea Turtles in Guinea-Bissau. *Chelonian Conservation and Biology* 8:150–160.

Delcroix, E., S. Bedel, G. Santelli and M. Girondot 2013. Monitoring design for quantification of marine turtle nesting with limited effort: a test case in the Guadeloupe archipelago. Oryx 48:1–11.

Donlan, C.J., D.K. Wingfield, L.B. Crowder and C. Wilcox 2010. Using Expert Opinion Surveys to Rank Threats to Endangered Species: A Case Study with Sea Turtles. *Conservation Biology* 24:1586–1595.

Dunlop, H.M. and J.G. Fitter 1979. A K-Ar and Sr-isotopic study of the volcanic rocks of the island of Príncipe, West Africa — Evidence for mantle heterogeneity beneath the Gulf of Guinea. *Contributions to Mineralogy and Petrology* 71:125–131.

Eckert, K.L. 1999. Designing a Conservation Program. P. 3 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois and M. Donnelly (Eds). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Esteban, N., J.A. Mortimer and G.C. Hays 2017. How numbers of nesting sea turtles can be overestimated by nearly a factor of two. Proceedings of the Royal Society, Biological Sciences 284:20162581.

Ferreira, R.L. 2015. Sea Turtle Artisans of São Tomé and Príncipe. *African Sea Turtle Newsletter* 3:25-33.

Ferreira, R.L. and H.R. Martins 2013. Nesting Hawksbill Turtle, *Eretmochelys imbricata*, Disorientation at a Beach Resort on Príncipe Island, West Africa. *Marine Turtle Newsletter* 136:7–9.

Ferreira, R.L., F.R. Ceia, T.C. Borges, J.A. Ramos, and A.B. Bolten 2018. Foraging niche segregation between juvenile and adult hawksbill turtles (*Eretmochelys imbricata*) at Príncipe island, West Africa. *Journal of Experimental Marine Biology and Ecology*:1-7.

Formia, A., B.J. Godley, J.-F. Dontaine, and M.W. Bruford 2006. Mitochondrial DNA diversity and phylogeography of endangered green turtle (*Chelonia mydas*) populations in Africa. *Conservation Genetics* 7:353–369.

Frazier, J.G. 1999. Community-Based Conservation. Pp. 15–19 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, amd M. Donnelly (Eds.). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Fretey, J. 2001. Biogeography and Conservation of Marine Turtles of the Atlantic Coast of Africa. CMS/MT-AFR.1/Inf.4, UNEP/CMS Secrertariat, Bonn, Germany 429 pp.

Gerrodette, T. and B.L. Taylor 1999. Estimating Population Size. Pp. 62–66 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K.L., K.A. Bjorndal, F.A. Abreu-grobois, and M. Donnelly (Eds). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Girondot, M. 2010. Estimating density of animals during migratory waves: a new model applied to marine turtles at nesting sites. *Endangered Species Research* 12:95–105.

Graff, D. 1996. Sea Turtle Nesting and Utilization Survey in São Tomé. *Marine Turtle Newsletter* 75:8–12.

Hays, G.C. and R. Scott 2013. Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Functional Ecology* 27:748–756.

Heithaus, M.R. 2013. Predators, prey, and the ecological roles of sea turtles. Pp. 249–284 in: The Biology of Sea Turtles, Vol. III. Wyneken, J., K.J. Lohmann and J.A. Musick (Eds.). CRC Press, Boca Raton, London, New York.

Honarvar, S., D.B. Fitzgerald, C.L. Weitzman, E.M. Sinclair, J.M.E. Echube, M. O'Connor, and G.W. Hearn 2016. Assessment of Important Marine Turtle Nesting Populations on the Southern Coast of Bioko Island, Equatorial Guinea. *Chelonian Conservation and Biology* 15:79–89.

Horrocks, J.A. and N.M. Scott 1991. Nest site location and nest success in the hawksbill turtle *Eretmochelys imbricata* in Barbados, West Indies.

Marine Ecology Progress Series 69:1–8.

Hydrographic Institute 1995. Principe Island Nautical Chart, 1:70000. Instituto Hidrográfico de Portugal, Ministério da Defesa Nacional, Marinha.

Jackson, A.L., A.C. Broderick, W.J. Fuller, F. Glen, G.D. Ruxton, and B.J. Godley 2008. Sampling design and its effect on population monitoring: How much monitoring do turtles really need?. *Biological Conservation* 141:2932–2941.

Juste, J. 1994. Etudes d'appui à l'aménagement et à la gestion des zones écologiques de Sao Tomé et Principe. Iième partie: Délimitation de la Zone Ecologique de Principe et correction des limites de Sào Tomé. Mimeograph, AGRECO-CTFT.

Kamel, S.J. 2013. Vegetation cover predicts temperature in nests of the hawksbill sea turtle: Implications for beach management and offspring sex ratios. *Endangered Species Research* 20:41–48.

Komar, P.D. 1976. Beach Processes and Sedimentation. XVII Edition. Prentice Hall, New Jersey, USA. 429pp.

Krieger, J. 2010. Home is Where the Triggers Are: Increasing Asthma Control by Improving the Home Environment. *Pediatric Allergy, Immunology, and Pulmonology* 23:139–145.

Loureiro, N., H. Carvalho, and Z. Rodrigues 2011. Praia Grande of Príncipe Island (Gulf of Guinea): an important nesting beach for the green turtle *Chelonia mydas*. *Arquipelago*. Life and Marine Sciences: 28:89–95.

Mason, J. 1994. Linking qualitative and quantitative data analysis. Pp. 89–110 in: Analyzing qualitative data. Bryman, A. and R.G. Burgess (Eds). Routledge.

Mazaris, A.D., G. Schofield, C. Gkazinou, V. Almpanidou, and G.C. Hays 2017. Global sea turtle conservation successes. *Science Advances* 3:e1600730.

Metcalfe, K., P.D. Agamboué, E. Augowet, F. Boussamba, F. Cardiec, J.M. Fay, A. Formia, J.R. Kema Kema, C. Kouerey, B.D.K. Mabert, et al. 2015. Going the extra mile: Ground-based monitoring of olive ridley turtles reveals Gabon hosts the largest rookery in the Atlantic. *Biological Conservation* 190:14–22.

Miller, J. 1997. Reproduction in Sea turtles. Pp. 51–81 in: The Biology of Sea Turtles, Vol. I. Lutz, P.L., and J.A. Musick (Eds). CRC Marine Science Series, CRC Press, Inc.

Monzón-Argüello, C., N.S. Loureiro, C. Delgado, A. Marco, J.M. Lopes, M.G. Gomes and F.A. Abreu-Grobois 2011. Príncipe island hawksbills: Genetic isolation of an eastern Atlantic stock. *Journal of Experimental Marine Biology and Ecology* 407:345–354.

Mortimer, J. and R. Bresson 1999. Temporal Distribution and Periodicity in Hawksbill Turtles (*Eretmochelys imbricata*) Nesting at Cousin Island, republic of Seychelles, 1971-1997. *Chelonian Conservation and Biology* 3:318–325.

Mortimer, J. and M. Donnelly 2008. *Eretmochelys imbricata*. The IUCN Red List of Threatened Species. IUCN SSC Marine Turtle Specialist Group. Available from http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T8005A12881238.en. [Accessed 24 November 2015].

Mortimer, J.A. 1999. Reducing Threats to Eggs and Hatchlings: Hatcheries. Pp. 175–178 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Mortimer, J.A. 1982. Factors influencing beach selection by nesting sea turtles. Pp. 45–51 in: Biology and Conservation of Sea Turtles. Bjorndal, K.A. (Ed.). Smithsonian Institution Press, Washington, D.C.

Mrosovsky, N. 2006. Distorting gene pools by conservation: Assessing the case of doomed turtle eggs. *Environmental Management* 38:523–31.

National Institute of Statistics 2013. IV Recenseamento Geral da População e da Habitação 2012 - Resultados Nacionais. Instituto Nacional de Estatística, São Tomé e Príncipe.

National Research Council 2010. Assessment of Sea-Turtle Status and Trends: Integrating Demography and Abundance. National Research Council, The National Academic Press:162 p.

Pritchard, P.C.H. and J.A. Mortimer 1999. Taxonomy, External Morphology, and Species Identification. Pp. 21–38 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K.L., K.A. Bjorndal, F.A. Abreu-Grobois, and M. Donnelly (Eds). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Regional Legislative Decree 2009. Decreto Legislativo Regional n.o 3/2009. Protecção e a conservação das tartarugas marinhas. Assembleia Regional, Região Autónoma do Príncipe, República Democrática de São Tomé e Príncipe.

Richardson, J.I., R. Bell, and T.H. Richardson 1999. Population Ecology and Demographic Implications Drawn From an 11-Year Study of Nesting Hawksbill Turtles, *Eretmochelys imbricata*, at Jumby Bay , Long Island , Antigua , West Indies. Chelonian *Conservation Biology* 3:244–250.

Schroeder, B. and S. Murphy 1999. Population Surveys (ground and aerial) on Nesting Beaches. Pp. 45–56 in: Research and Management Techniques for the Conservation of Sea Turtles. Eckert, K.L., K.A.

Bjorndal, A.F. Abreu-Grobois and M. Donnelly (Eds.). IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Solow, A.R., K.A. Bjorndal, and A.B. Bolten 2002. Annual variation in nesting numbers of marine turtles: the effect of sea surface temperature on re-migration intervals. *Ecology Letters* 5:742–746.

Tomás, J., B.J. Godley, J. Castroviejo, and J.A. Raga 2010. Bioko: Critically important nesting habitat for sea turtles of West Africa. *Biodiversity and Conservation* 19:2699–2714.

Vieira, S., B.F. Airaud, V. Jiménez, D. Monteiro, and J.C. do Rio 2017a. Local Fishermen Participating in Sea Turtle In-water Data Collection in São Tomé Island. *African Sea Turtle Newsletter* 8:36–38.

Vieira, S., B.F. Airaud, V. Jiménez, F. Airaud, D. Monteiro, and A.B. Jesus 2017b. Seeking a Better Future for Women Traders and Sea Turtles in São Tomé and Príncipe. *African Sea Turtle Newsletter* 8:33–35.

Wallace, B.P., A.D. DiMatteo, A.B. Bolten, M.Y. Chaloupka, B.J. Hutchinson, F.A. Abreu-Grobois, J.A. Mortimer, J.A. Seminoff, D. Amorocho, K.A. Bjorndal, et al. 2011. Global conservation priorities for marine turtles. *PLOS One* 6:e24510.

Weber, N., S.B. Weber, B.J. Godley, J. Ellick, M. Witt, and A.C. Broderick 2013. Telemetry as a tool for improving estimates of marine turtle abundance. *Biological Conservation* 167:90–96.

Weber, S.B., N. Weber, J. Ellick, A. Avery, R. Frauenstein, B.J. Godley, J. Sim, N. Williams, and A.C. Broderick 2014. Recovery of the South Atlantic’s largest green turtle nesting population. *Biodiversity and Conservation* 23:3005–3018.

Wentworth, C.K. 1922. A Scale of Grade and Class Terms for Clastic Sediments. *The Journal of Geology* 30:377–392.

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APPENDIX

General beach characteristics for the 50 sandy beaches identified at Príncipe Island (*obstacles on the beach preventing sea turtle nesting; **rocks on the foreshore precluding green turtle emergences), including estimated clutch densities (clutches/km, based on the suitable length) for the 2009/10 nesting season, for both hawksbills (*Ei*) and green turtles (*Cm*). N and S are north and south areas of Principe, respectively.

#	Beach name	Area	Lat, Long	Total length (m)	Suitable length (m)	Sand color	Grain size	Clutch density *Ei*	Clutch density *Cm*
1	Papagaio	N	1.641 / 7.423	545	245	brown	small	0	0
2	Hospital Velho	N	1.644 / 7.429	106	38	brown	small	0	0
3	Ponta Mina	N	1.646 / 7.436	158	38	brown	small	0	0
4	Évora (a)	N	1.645 / 7.439	162	9	yellow	small	0	0
5	Évora (b)	N	1.642 / 7.441	447	53	yellow	small	0	0
6	Portinho	N	1.638 / 7.446	553	236	yellow	small	0	0
7	Salgado	N	1.633 / 7.452	167	93	light brown	medium	0	0
8	Abade	N	1.631 / 7.456	256	199	brown	medium	0	0
9	D'Areia	S	1.608 / 7.432	295	52	light brown	medium	0	125.9
10	Bumbo (Abelha)	S	1.604 / 7.426	566	319	yellow	small	19.1	224.1
11	Espraínha	S	1.597 / 7.424	152	57	yellow	small	0	382.7
12	Cemitério	S	1.569 / 7.426	406	153	yellow	medium	16	133.7
13	Cabinda	S	1.564 /7.422	209	86	yellow	small	28.6	369.6
14	Infante (Grande)	S	1.558 / 7.417	965	510	brown	small	17.2	564.9
15	Infante	S	1.556 / 7.411	366	77	dark brown	medium	76	467.7
16	Seca	S	1.546 / 7.399	417	246	yellow	coarse	12.8	331.6
17	Candeia*	S	1.540 / 7.398	157	17	dark brown	small	0	0
18	Rio Porco	S	1.550 / 7.376	273	57	dark brown	coarse	110.9	357.8
19	Rio São Tomé	S	1.560 / 7.355	427	225	light brown	small	40	318.5
20	Novo (Formiga)	S	1.595 / 7.337	94	12	yellow	coarse	0	170.6
21	Maria Correia	S	1.601 / 7.353	169	90	brown	coarse	0	0
22	Lapa	S	1.605 / 7.364	391	247	dark brown	medium	0	0
23	Caixão	N	1.619 / 7.370	760	235	brown	medium	0	0
24	Praínha (a)	N	1.631 / 7.368	279	25	light brown	medium	0	0
25	Praínha (b)	N	1.632 / 7.367	69	35	light brown	coarse	0	0
26	Iola	N	1.647 / 7.373	491	300	yellow	medium	8.1	6.8
27	Pedra Furada	N	1.656 / 7.369	165	66	brown	medium	0	29.3
28	Ponta Pedra Furada**	N	1.657 / 7.367	77	77	yellow	coarse	150	0
29	Ponta Marmita**	N	1.683 / 7.372	95	81	yellow	coarse	150.7	0
30	Margarida	N	1.681 / 7.373	127	75	yellow	coarse	0	81.9
31	Sundi	N	1.679 / 7.380	548	354	light brown	coarse	6.9	0
32	Barraca	N	1.680 / 7.384	199	144	light brown	medium	0	14.2
33	Mocotó	N	1.681 / 7.390	522	459	light brown	medium	5.3	31.2
34	Ribeira Izé	N	1.685 / 7.395	610	399	light brown	medium	6.1	35.9
35	Côco	N	1.691 / 7.401	611	400	light brown	medium	5.8	14.5
36	Bom-bom*	N	1.695 / 7.402	202	20	light brown	medium	0	0
37	Santa Rita	N	1.691 / 7.405	794	470	light brown	medium	0	8.2
38	Seabra	N	1.689 / 7.412	158	130	brown	medium	0	15.8
39	Cana (Lagaia)	N	1.687 / 7.419	120	56	brown	medium	0	0

#	Beach name	Area	Lat, Long	Total length (m)	Suitable length (m)	Sand color	Grain size	Clutch density	
								Ei	***Cm***
40	Campanha	N	1.684 / 7.426	293	290	light brown	small	0	8.9
41	Popa (Sandida)	N	1.686 / 7.429	134	78	yellow	coarse	0	26.3
42	Burra	N	1.684 / 7.435	1222	815	yellow	medium	0	0
43	Banana	N	1.690 / 7.442	231	213	yellow	coarse	28.2	75.8
44	Franguinha	N	1.684 / 7.449	374	242	light brown	medium	0	8
45	Armazén	N	1.682 / 7.453	334	261	light brown	medium	11.5	51.6
46	Macaco	N	1.681 / 7.456	159	128	light brown	medium	0. 0	21
47	Boi	N	1.680 / 7.460	289	277	yellow	coarse	10.8	106.9
48	Uba	N	1.674 / 7.459	80	45	yellow	coarse	66.7	0
49	Paciência (Grande)	N	1.671 / 7.447	1500	1255	yellow	medium	4.8	251
50	Capitania	N	1.643 / 7.421	62	19	brown	small	0	0