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Seasonal factors affecting sea turtle nesting in the Southeastern Caribbean Sea (Gulf of Paria, Venezuela)

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ABSTRACT

The nesting characteristics (number of nests and eggs, time of year, nesting initiation, and nesting length) of leatherback (*Dermochelys coriacea*) and hawksbill (*Eretmochelys imbricata*) sea turtles of the southern Caribbean Sea (specifically in the Gulf of Paria in Venezuela), were examined in association with weekly precipitation averages and number of rainy days per week during the period between 2009 and 2018. We hypothesized about the influence of rainfall intensity and patterns as the main abiotic factor for sea turtle nesting. On average, leatherbacks preferred nesting during the drier season of each year (March, April, and May), while hawksbills nested during the rainy season (June to September). For both species, we found few significant correlations between the number of nests or clutch size (number of eggs per nest) and weekly averages of seasonal precipitation rates in the region. Average hawksbill clutch sizes were not correlated with average precipitation rates but were positively correlated with the number of rainy days per week ($r=0.66$, $P\lesssim0.05$). Average hawksbill clutch sizes decreased each year on average (-3.3 eggs/year, $r=-0.88$, $P\lesssim0.001$), which coincided with a negative long-term trend in the number of rainy days (-0.11 rainy days/week, $r=-0.69$, $P\lesssim0.05$). During the study period, nesting activities for both leatherback and hawksbills started progressively later (0.9 and 0.6 weeks/year, respectively $p\lesssim0.05$) and were shorter (-0.9 and -0.8 weeks /year, $P\lesssim0.1$ and $P\lesssim0.05$, respectively).

Descriptors: Rainfall, Sea turtles, Remote sensing, Seasonal nesting, Fecundity.

INTRODUCTION

Sea turtles need specific environmental conditions for nesting in order to increase the chances of successful incubation of the eggs they bury in sandy beaches (Mortimer 1990, Wood & Bjorndal 2000, Pike 2013). Turtles seek specific beach sand characteristics, but nesting is also affected by the seasonal conditions such as temperature and rainfall (Maulany *et al.* 2012, Rafferty *et al.* 2017). Understanding this dependence on specific environmental conditions is important for planning management strategies under future climate scenarios (Patricio *et al.* 2021).

Sand moisture and precipitation are likely to be important factors in determining when loggerhead (*Caretta caretta*) and hawkbill (*Eretmochelys imbricata*) sea turtles nest (McGehee 1990, Hitchins

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et al. 2003). Hatchling success for leatherback turtle (*Dermochelys coriacea*) clutches is negatively affected by intense rainfalls (Houghton *et al*. 2007), while leatherback hatchling success is also affected by rainfall on a global scale (Santidrian *et al.* 2015). Saragoça *et al.* (2020) found a positive correlation between precipitation during February (dry season) between 1987 and 2015 and increased green turtle (*Chelonia mydas*) clutch numbers in Tortuguero, Costa Rica. This positive relationship was accentuated by higher/lower precipitation and larger/smaller clutch numbers during El Niño/La Niña events.

Rain directly affects sand temperature, refreshing and cooling the substrate (McGehee 1990). A consequence of temperature change can be alterations in the hatchling sex ratio of loggerhead turtles (*Caretta caretta*) (Lolavar & Wyneken 2015, Lolavar & Wyneken 2017). Heavy rainfalls can lead to lower incubation temperatures, as observed in a South Pacific green turtle rookery which produced 54% male hatchlings between season 2007 until season 2019 (Laloë *et al.* 2020). A similar pattern was observed for hawksbills in the northern Australia Great Barrier Reef (Staines *et al.* 2020).

In this work, we hypothesized about the possible influence of rainfall intensity and patterns on the number of nests and clutch size for hawksbill and leatherback sea turtles along the southern shores of the Paria Peninsula (Venezuela), in the southeastern Caribbean Sea. The prediction was that certain pluviometry variables correlate with nest numbers and clutch size for each species. This study complements an earlier study on the impact of human activities on nesting variability around the periphery of the Gulf of Paria, in which only nest numbers were considered (Balladares & Quintero-Torres 2019). Finally, here we consider only rainfall, not temperature, as the primary abiotic factor affecting nesting.

METHODS

Study Area

The Gulf of Paria is an estuarine region in the southeastern Caribbean Sea, with the Orinoco River delta to the south. It is located south of the Paria peninsula, between Venezuela and Trinidad (Figure 1; Rincon *et al.* 2008). Along the southern border of the Paria peninsula, there are several

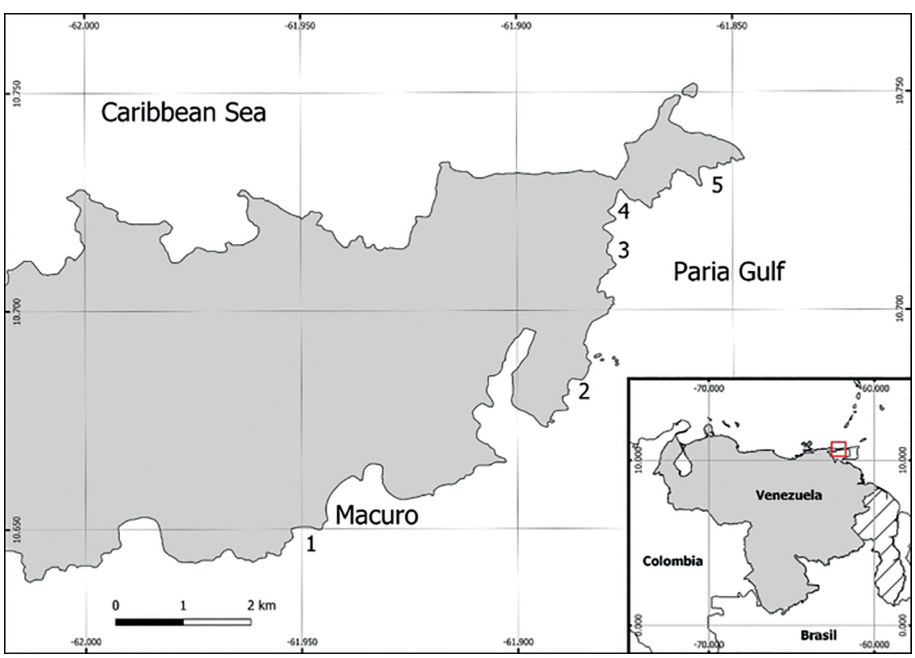

Figure 1. Location of the main nesting beaches along the southeastern Caribbean Sea in the Gulf of Paria, Venezuela. The beaches monitored in this study were (1) Macurito, (2) Los Garzos, (3) Silvano, (4) Obispo, and (5) Cerezo.

small beaches that are regularly used by sea turtles for nesting (Figure 1; Balladares & Dubois 2010). These beaches are: 1) Macurito, 2) Los Garzos, 3) Silvano, 4) Obispo, and 5) Cerezo. The beaches are narrow, as the coast features a steep terrain. Typical beaches are approximately less than 300 m long and 50 m wide. The fives beaches sampled are sandy with low berm, and covered with supra-littoral vegetation of manchineel (*Hippomane mancinella* L.) and portia trees (*Thespesia populnea* L.). Beaches 2, 3, 4, and 5 are inside the Peninsula de Paria National Park. Macurito beach is outside the park and near the fishing town of Macuro.

Field work

Surveys began in 2003, from mid-March though the end of October, and were conducted each year through 2021. Each site was visited four times per week during the day, and during the night (between 8 pm and 4 am) at Los Garzos beach. Beach patrols were performed with at least two local trained patrollers assigned to the main nesting grounds of playa Los Garzos and Macurito. All females emerging from the sea to nest were identified by species, measured, and photographed. Turtles were also tagged when possible. Special care was taken in counting eggs in new nests each night. Starting in August 2006, once a proper and secure hatchery was built in the town of Macuro, we moved all nests from their original beaches to the hatchery to avoid predation and poaching. By 2007, we had expanded the search to all five beaches (Balladares & Dubois 2014). During 2012, 2017, and 2018, we were unable to translocate the eggs due to maintenance and expansion of the hatchery. During those years, we intensified patrolling of the beaches. Natural and translocated nests were counted for clutch size and emergence success. Hatchlings were then set free on the beaches where the eggs had been laid if possible, or on Macuro, where the hatchery was located.

Precipitation Datasets and Processing

Precipitation records from regional meteorological stations are irregular and with an unknown uncertainty because of continuously changing observation methods and poor stations maintenance. We therefore used rainfall estimates from the Multi-Satellite Precipitation Analysis (TMPA V7), which merges rainfall estimates from several satellites with gauge data (Huffman *et al.* 2007). We specifically downloaded the TMPA-V7 3B42 product from NASA (https://pmm.nasa.gov/data-access/downloads/trmm). This provided daily-accumulated precipitation with a spatial resolution of 0.25 degrees (~28 km). We extracted the precipitation data over the Gulf of Paria, off the distal part of the Paria peninsula (10.625°N - 61.875°W). We calculated weekly precipitation averages and counted the number of rainy days during the week to compare with the weekly sea turtle nest data.

The TMPA-V7 3B42 dataset provides three products: ‘Precipitation’ (Surface Precipitation Estimate), ‘IR-precipitation’ (Infrared Precipitation Estimate), and ‘HQ-precipitation’ (Microwave Precipitation Estimate). In order to identify which product was closest to in-situ precipitation data, we compared weekly averages from each satellite products with the weekly average precipitation from the Piarco Meteorological Station in Trinidad for the period 1998-2015 (10.61°N and 61.35°W) located ~60 km east from the center of the grid cell of the satellite dataset (Piarco meteorological data moved to http://www.metservice.gov.tt/climate_data/Piarco_view.php). The highest correlation was found with ‘Precipitation’ (r = 0.58, R^2=0.34, *slope*=0.43, $P<0.001$, n=902; ‘IR-precipitation’ and ‘HQ-precipitation’ showed R^2 = 0.30 and 0.21, respectively). The weekly averages of TMPA ‘Precipitation’ shows the same seasonality as the *in-situ* Piarco data (Fig. 2a). The TMPA ‘Precipitation’ averages, however, underestimated the magnitude of in-situ precipitation (weekly satellite precipitation is approximately 63% of the weekly *in-situ* precipitation at Piarco). Long-term averages and standard deviations for the weekly time series were 126.7 ± 133.6 mm/day for TMPA ‘Precipitation’. The similarity in their seasonality and the high standard deviations of both datasets are the reason why only 10 of 52 climatological weekly averages showed significant differences between the in-situ and satellite precipitation (paired student’s t-test $P<0.05$, Fig.

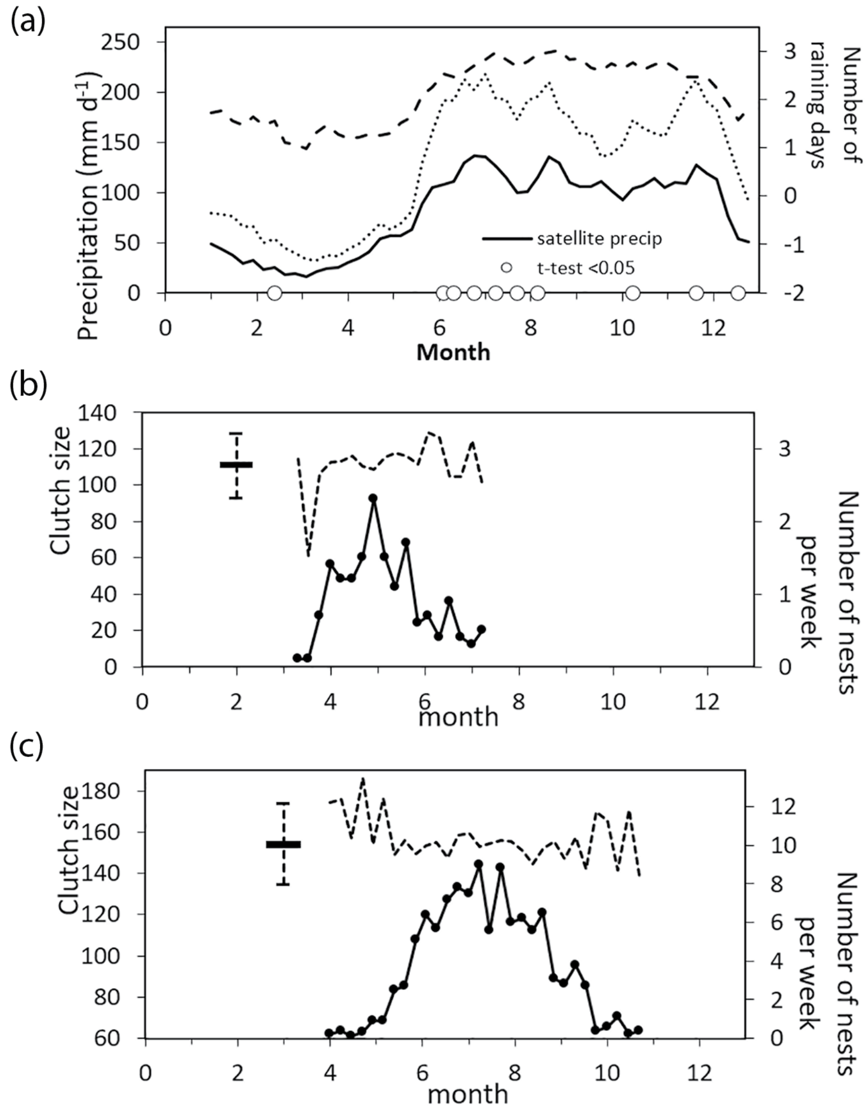

Figure 2. Long term weekly averages of (a) satellite average precipitation and number of rainy days per week over the study area (10.625°N - 61.875°W, 1998-2018), and *in-situ* precipitation from a meteorological station located 60 km east of the study area (Piarco, Trinidad & Tobago, 1998-2015). Comparison between the weekly time series of satellite and *in-situ* precipitation (paired Student's *t*-test $P<0.05$) showed only 10 weeks with significant differences (white circles). Weekly averages of the number of nests and the average clutch size per nest (2009-2018) for (b) leatherback, *Dermochelys coriacea* and (c) hawksbill, *Eretmochelys imbricata*. For each species, the total time series clutch size average per nest ± 1 SD are shown for comparison with the weekly averages. The smallest clutch size of leather back during the middle of March comes from only one nest during the entire time-series.

2a). The precipitation product TMPA-V7 has been found to systematically underestimate or overestimate rainfall in different climatic regions (Yong *et al.* 2014, Qiao *et al.* 2014, Guo *et al.* 2015). At other locations close to our study area, such as off French Guiana and the north region of Brazil, the satellite precipitation products also tend to underestimate precipitation. However, the TMPA-V7 product performed better than other satellite precipitation products (Ringard *et al.* 2015). Given these results, we chose the 'Precipitation' product for our analyses.

Statistical Analyses

For the analysis we used the number of nests per beach (excluding poached or lost) and clutch size for leatherbacks and hawksbills in new nests, counted daily. We analyzed sea turtle data from 2009 to 2018 due to the more systematic sampling of all five beaches during this period. Weekly averages and climatology (2009-2018) were calculated for the number of nests and clutch sizes. Precipitation was averaged weekly for the same decade, and the number of days with rainfall for each week was recorded. Annual seasonal summaries for all variables during the nesting seasons of leatherbacks and hawksbills are presented in Tables 1 and 2.

The first and the last nesting weeks of the entire study period were used to define the nesting season for each species. For leatherbacks, this was on average from mid-March to mid-July (weeks 11 to 28), while for hawksbills, this was from April to mid-October (weeks 14 to 43).

Possible associations between each species' nesting parameters and the precipitation variables were explored using linear partial correlation models in MATLAB (2014). We used partial correlation to check the association between the dependent variable with each predictor after adjusting for the other variables, to avoid misleading results should there be a confounding variable related to both the dependent and independent variables. We analyzed the possible relationships between the number of nests and clutch size (which reflects fecundity) and between these variables and weekly average rainfall and number of rainy days during the week. We used regression and correlation (Zar 2010, Legendre & Legendre 2012) to analyze these relationships, producing estimates for the total time series and for each year studied.

RESULTS

General seasonal pattern for each species and satellite data

The satellite precipitation records (Figure 2a) show a short dry season between February and early April (Weeks 4-15) for the study area. There is a transition period between mid-April to May with increasing precipitation, and a lengthy rainy season between mid-June and November (Weeks 24-49) with some variability. The number of rainy days during the week was proportional to precipitation with similar seasonality: up to 1 rain day per week during the dry season, and 2.5-3 rain days per week during the peak of the rainy season.

Leatherbacks had an earlier and shorter nesting season compared to hawksbills. The weekly nesting climatology (Figure 2b) shows the start of the nesting season for the leatherbacks as early as Week 11 and up to Week 28 (March to mid-July). Leatherback nesting peaks between mid-April and mid-May (Weeks 15-20; ~1.5-2 nests per week). The leatherback nesting season peaks during the transition from dry to rainy season; when precipitation and number of rainy days peaks, leatherback nesting season is ending. The long-term (2009-2018) weekly average number of nests was 2.5 ± 2.1*SD* per week (Table 1). The clutch size of leatherbacks did not show seasonality, though an apparent higher variability in weekly clutch size averages occurred at the beginning and end of the nest season, when there were fewer nests (Table 1). In general, the weekly averages of leatherbacks clutch sizes per nest are within 110.8 ± 17.7 eggs per nest (Figure 2b and Table 1).

Hawksbill nesting season length was over twice as long as that of leatherbacks (Table 2), lasting from 19 weeks (2018) to 29 weeks (2013), with an average nesting season of 22.8 weeks. On average, ~83% of the weeks during the hawksbill nesting season saw new nests. The start and end of hawksbill nesting season was less variable, with ranges of 8 and 6 weeks, respectively (Table 2). Nesting season began between Week 14 (2010) and Week 22 (2016), with an average starting week of 17.6. The season ended between Week 37 (2011) and Week 43 (2013), with an average ending week of 39.4. On average, new nests were identified during 83% of the weeks during the nesting season. The beginning of hawksbill nesting season coincided with increasing precipitation and number of rainy days during the transition period, and the nesting peak coincided with the first two peaks of the rainy season (Fig. 2c). The weekly climatology shows that hawksbills started nesting as early as Week 14 week and up to Week 43

Table 1. Summary of variables obtained during the leatherback (*Dermochelys coriacea*) nesting season from mid-March to mid-July. The earliest and latest nesting weeks for the study period defined the "nesting season" (weeks 14^{th} to 43^{th}). Values shown are for each year and for the entire time series (2009-2018). Weekly rainy days averages and precipitation averages (mm d^{-1}) were calculated for the entire season, and for the weeks with and without. (*) Where there were more than one week with the highest seasonal number of nests, the values shown are for the first week.

	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	All Years
Number of nests per week											
Seasonal máximum	10	3	5	3	4	3	2	4	-	5	10
Seasonal sum	69	14	21	11	13	17	5	7	-	9	166
Average	4.3	2.0	2.6	1.5	1.6	1.8	1.2	2.3	-	2.2	2.5
Standard deviation	3.2	0.6	1.6	0.8	1.1	0.8	0.5	1.5	-	1.9	2.1
Clutch size per nest											
Minimum	83	99	73	61	87.5	93.5	44	104.8	-	90	44
Maximum	130	135	135.5	137	119	148.5	129	129	-	107.6	148.5
Average	112.7	117.6	111.2	104.4	106.7	118.2	95.4	119.9	-	102.2	110.8
Standard deviation	12.4	13.2	20.0	25.6	9.7	17.3	36.3	13.2	-	8.3	17.7
Nesting season											
First week with nests	11	13	13	12	14	14	16	24	-	16	11
Last week with nests	28	22	25	21	23	26	21	28	-	25	28
Season length	18	10	13	10	10	13	6	5	-	10	-
Number of weeks with nests	16	7	8	7	8	9	4	3	-	4	-
Number of weeks with no-nests	2	3	5	3	2	4	2	2	-	6	-
Week with the highest nest number (*)	19	25	18	18	27	21	18	28	-	30	-
Precipitation during nesting weeks											
Minimum	0.0	0.0	16.3	0.0	0.0	0.0	0.0	26.8	-	10.4	0.0
Maximum	120.6	472.9	287.4	276.3	338.5	198.4	63.3	306.5	-	309.5	472.9
Average	43.2	133.2	102.8	101.9	84.6	56.2	30.3	137.8	-	98.4	79.8
Standard deviation	34.2	169.2	97.2	103.6	114.7	62.1	35.1	148.5	-	141.3	98.2
Precipitation during the maximum nesting week	67.9	472.9	287.5	139.6	57.9	3.7	0.0	306.5	-	309.5	-
Precipitation during no-nesting weeks											
Minimum	0.0	0.0	11.7	8.8	5.6	0.0	0.0	0.0	-	0.0	0.0
Maximum	0.0	229.5	331.6	227.8	262.7	127.2	214.5	639.8	-	382.8	639.8
Average	0.0	69.1	98.4	77.4	68.6	44.8	49.9	93.2	-	63.9	68.9
Standard deviation	0.0	80.3	102.8	75.7	83.3	41.5	78.1	179.0	-	102.9	107.5
Precipitation for the whole nesting season											
Seasonal mínimum	0.0	0.0	11.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Seasonal máximum	120.6	472.9	331.6	276.3	338.5	198.4	214.5	639.8	564.5	382.8	639.8
Seasonal average	38.4	94.0	100.4	86.9	75.7	50.5	45.5	100.6	66.0	71.6	72.9
Seasonal standard deviation	35.1	122.2	97.4	85.5	95.7	51.6	70.4	171.1	134.9	108.8	104.0
Number of rainy days during nesting weeks											
Minimum	0	0	1	0	0	0	0	1	-	1	0
Maximum	3	4	4	5	5	3	2	5	-	5	5
Average	1.4	1.4	2.3	2.3	1.9	1.8	1.0	2.7	-	2.0	1.8
Standard deviation	0.8	1.3	1.0	1.8	1.9	0.9	1.2	2.1	-	2.0	1.3
Number of rainy days during the maximum nesting week (*)	2	4	1	4	1	2	0	5	-	5	-
Number of rainy days during no-nesting weeks											
Minimum	0	0	1	1	1	0	0	0	-	0	0
Maximum	0	5	5	5	3	3	3	5	-	3	5
Average	0.0	2.4	3.0	2.2	2.0	1.7	0.9	1.6	-	1.0	1.7
Standard deviation	0.0	1.6	1.3	1.2	0.9	1.1	0.9	1.4	-	1.0	1.4
Number of rainy days for the whole nesting season											
Seasonal mínimum	0	0	1	0	0	0	0	0	0	0	0
Seasonal máximum	3	5	5	5	5	3	3	5	4	5	5
Seasonal average	1.3	2.0	2.7	2.2	1.9	1.7	0.9	1.8	1.3	1.2	1.7
Seasonal standard deviation	0.9	1.5	1.3	1.4	1.4	1.0	0.9	1.5	1.4	1.3	1.3

Table 2. Summary of variables obtained during the hawksbill (*Eretmochelys imbricata*) nesting season from April to mid-October. The earliest and latest nesting weeks for the whole study period was consider the “nesting season” (weeks 14th to 43th). Values shown for each year and for the whole time series (2009-2018). Weekly rainy days averages and precipitation averages (mm d^{-1}) were calculated for the whole season, and for the weeks with nests and the weeks with no--nests. (*) In case there were more than one week with the highest seasonal number of nests, the values shown are for the first week.

	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	All Years
Number of nests per week											
Seasonal máximum	16	9	17	12	12	23	19	16	12	16	23
Seasonal sum	105	107	124	109	146	183	94	102	56	79	1105
Average	4.8	4.3	6.5	5.2	5.6	9.2	5.5	5.7	4.7	7.2	5.8
Standard deviation	3.9	2.7	4.9	3.3	3.6	5.7	4.8	3.9	3.1	5.6	4.3
Clutch size per nest											
Minimum	110.3	134	113.5	126	139	128.5	109	109	95.5	115.5	95.5
Maximum	199	209	203	190.33	189.5	167.3	184	191	145	183	209
Average	159.2	167.7	159.5	157.0	161.1	152.9	145.1	142.1	129.6	141.9	153.9
Standard deviation	19.9	15.7	20.6	13.3	13.4	10.7	21.3	20.9	15.1	19.5	19.6
Nesting season											
First week with nests	15	14	17	19	15	18	18	22	18	20	14
Last week with nests	40	41	37	40	43	38	37	42	38	38	43
Season length	26	28	21	22	29	21	20	21	21	19	-
Number of weeks with nests	22	25	19	21	26	20	17	18	12	11	-
Number of weeks with no-nests	4	3	2	1	3	1	3	3	9	8	-
Week with the highest nest number (*)	34	25	28	37	27	33	28	26	38	30	-
Precipitation during nesting weeks											
Minimum	0.0	0.0	11.7	0.5	0.0	0.0	0.0	0.0	13.1	0.0	0.0
Maximum	268.5	472.9	366.3	349.8	284.4	338.4	214.5	360.7	564.5	309.5	564.5
Average	84.9	135.7	122.1	109.6	86.3	91.9	76.9	103.7	119.6	103.1	103.2
Standard deviation	69.9	118.8	111.8	91.3	79.8	94.8	80.6	119.9	152.2	104.1	101.1
Precipitation during the maximum nesting week (*)	218.4	204.8	101.1	0.5	33.8	13.2	0.0	0.0	218.6	92.6	-
Precipitation during no-nesting weeks											
Minimum	0.0	0.0	22.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maximum	152.6	329.0	247.9	276.3	338.5	583.9	143.2	639.8	302.6	382.8	639.8
Average	37.1	76.1	71.2	90.9	86.6	96.9	44.6	103.7	75.0	95.6	78.8
Standard deviation	51.6	141.7	68.7	90.0	167.9	177.6	50.4	180.6	82.0	125.9	114.5
Precipitation for the whole nesting season											
Seasonal mínimum	0	0	11.7	0	0	0	0	0	0	0	0.00
Seasonal máximum	268.5	472.9	366.3	349.8	338.5	583.9	214.5	639.8	564.5	382.8	639.8
Seasonal average	72.2	125.8	103.4	104.0	86.3	93.6	62.9	103.7	92.9	98.4	94.3
Seasonal standard deviation	68.2	122.3	100.0	89.8	91.6	125.2	70.0	144.2	115.0	116.6	106.6
Number of rainy days during nesting weeks											
Minimum	0	0	1	1	0	0	0	0	1	0	0
Maximum	5	6	6	6	5	6	4	5	4	5	6
Average	2.3	2.8	2.6	2.6	2.3	2.4	1.4	2.2	2.1	1.6	2.3
Standard deviation	1.2	1.6	1.4	1.5	1.3	1.5	1.2	1.7	1.0	1.5	1.5
Number of rainy days during the maximum nesting week (*)	2	2	2	1	1	2	0	0	3	1	-
Number of rainy days during no-nesting weeks											
Minimum	0	0	2	0	0	0	0	0	0	0	0
Maximum	4	5	5	5	5	4	3	5	5	6	6
Average	1.8	2.6	3.3	2.6	1.8	1.60	1.2	1.7	1.8	1.8	1.9
Standard deviation	1.4	2.1	1.0	1.6	2.2	1.4	0.9	1.4	1.6	1.6	1.5
Number of rainy days for the whole nesting season											
Seasonal mínimum	0	0	1	0	0	0	0	0	0	0	0
Seasonal máximum	5	6	6	6	5	6	4	5	5	6	6
Seasonal average	2.1	2.8	2.9	2.6	2.2	2.1	1.2	1.9	1.9	1.7	2.2
Seasonal standard deviation	1.3	1.6	1.3	1.5	1.4	1.5	1.1	1.6	1.4	1.6	1.5

(mid-March to mid-October, Fig. 2c), with a nesting peak of approximately eight nests per week occurring between June-August (Weeks 22-34). The long-term (2009-2018) weekly average number of nests during hawksbill nesting season was 5.8 ± 4.3 per week (Table 2). Similar to leatherbacks, hawksbill clutch sizes did not show seasonality and showed higher apparent variability at the beginning and end of the nest season, when there were fewer nests (Table 2). However, those weekly averages are within 1.5 standard deviations of the long-term average (154.0 ± 19.6 eggs per nest, Table 2).

The weekly time series of satellite-derived precipitation observations (Figure 3a) showed values oscillating between 0 to 640 mm d^{-1}, with high precipitation variability during the rainy season. No long-term trends for weekly precipitation nor weekly number of rainy days were observed.

Figure 3b and 3c illustrate the annual number of nests and clutch size for 2009-2018. Leatherbacks laid over twice the number of nests during 2009 than during the rest of the series. We did not detect nests during 2017, but there was no unusual precipitation during that period (Figure 3a). The weekly time series of hawksbill clutch size showed a significant negative long-term trend of -3.3 eggs per year (Figure 3c, r= -0.45, R^2=0.21, P<0.01, slope= -3.29, n= 191), while none of the other weekly time series parameters showed any significant trend.

Annual correlations of nesting vs. rainfall

For each study year, the partial correlations did not show any significant associations between the number of nests or clutch sizes of leatherbacks with weekly rainfall or number of rainy days (Table 3). During 2009, leatherbacks had an exceptionally

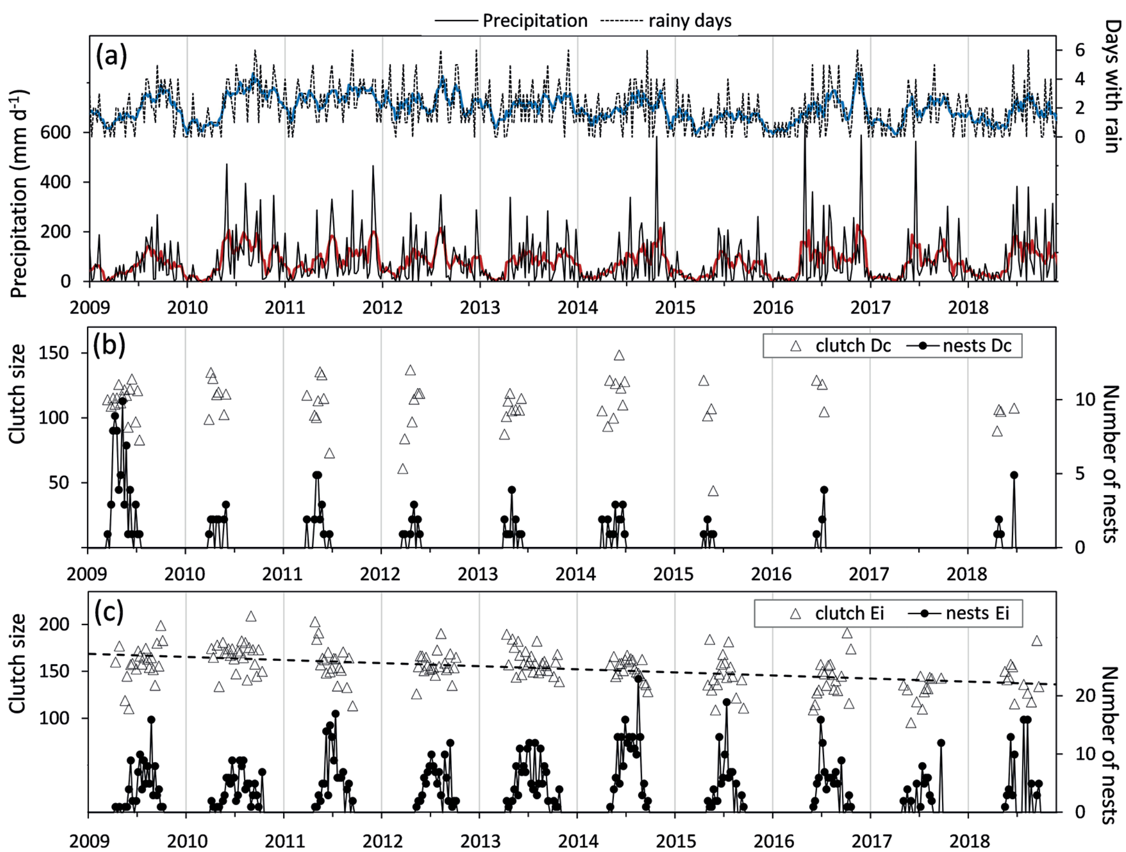

Figure 3. Time-series (2009-2018) of (a) weekly averages of satellite precipitation and weekly number of days with rain, and five-week moving-averages for precipitation (red) and rainy days (blue). Number of nests per week and weekly averaged clutch size for (b) leatherback and (c) hawksbill. The clutch size of hawksbill showed a significant negative long-term trend of -3.3 eggs per year (dashed line, R^2 0.21, P<0.01, n=191); the other parameters did not show any long-term trend.

Table 3. Partial correlations in a probability distribution of four variables: mean daily precipitation in a week, number of rainy days in a week, number of nests per week, and average clutch size per week, for Leatherback (*Dermochelys coriacea*). The values shown in the cells are the partial correlation coefficients. The asterisks indicate the level of significance of the two-tailed test; * P < 0.1, ** P < 0.05, *** P < 0.01. The values used for the calculations were those of the weeks with nests; the number of these weeks is n. Years 2015 to 2018 did not have enough weeks with nests to calculate partial correlations.

Partial correlations						
	2009 *n*=16	**2010** *n*=7	**2011** *n*=8	**2012** *n*=7	**2013** *n*=8	**2014** *n*=9
Between precipitation and						
rainy days	0.479 *	0.967 ***	0.833 **	0.893 **	0.538	0.287
number of nests	-0.441	0.385	-0.134	-0.527	-0.333	0.029
clutch size	0.267	-0.821 *	-0.669	0.741	-0.277	0.690 *
Between rainy days and						
number of nests	0.155	-0.195	-0.091	0.576	0.235	0.049
clutch size	-0.396	0.702	0.319	-0.818 *	0.781 *	-0.183
Between number of nests and						
clutch size	0.270	0.682	-0.173	0.576	-0.321	-0.035

long nesting season (12 weeks compared to an average of 5.5 weeks during the rest of the study period); it follows that 2009 was the year with the largest number of nests. However, there was no apparent relationship between number of nests and rainfall in any year. Clutch size and precipitation were only correlated during 2010 (negatively) and 2014 (positively), albeit with opposite signs. Clutch size was significantly correlated to number of rainy days per week during 2012 (negatively) and 2013 (positively). Again the signs of the correlations were opposite in those years.

Hawkbill nest count per week and clutch size were positively correlated with precipitation during 2009 and with rainy days during 2010. Clutch size was positively correlated with precipitation only in 2014 and negatively correlated with rainy days (Table 4).

Tables 3 and 4 also show the partial correlations between number of nests and clutch size for each species. There were no significant correlations between those two variables in any season nor for the entire study period. This means that the hypothesis of a relationship between these fecundity parameters and precipitation is not supported.

Seasonal correlations

We applied multiple correlation analysis on the seasonal average precipitation (and number of rainy days) averaged for each species nesting season and for the weeks with nests and the weeks of no nesting (Tables 3 and 4), but found no statistical differences between those averages using the Welch's *t*-test, implying that rainy conditions during the rainy seasons were similar for weeks with and without nesting (Table 5a).

The analysis of seasonal parameters showed statistically significant long-term trends for these and other variables (Table 5b). The hawksbill clutch size showed a negative long-term trend (Figure 3c; regression parameters b= -3.35 eggs per year, r= -0.88, P ≤0.01, n=10) when using the complete weekly time series; the regression parameters were b= -3.29, r= -0.45, P ≤0.01, n= 191. Long-term trends calculated with seasonal

Table 4. Partial correlations in a probability distribution of four variables: mean daily precipitation in a week, number of rainy days in a week, number of nests per week, and average clutch size per week, in the Hawksbill (*Eretmochelys imbricata*). The values shown in the cells are the partial correlation coefficients. The asterisks indicate the level of significance of the two-tailed test; *P < 0.1, ** P < 0.05, *** P < 0.01. The values used for the calculations were those of the weeks with nests; the number of these weeks is *n*.

Partial correlations	2009 *n*=16	2010 *n*=25	2011 *n*=19	2012 *n*=21	2013 *n*=26	2014 *n*=20	2015 *n*=17	2016 *n*=18	2017 *n*=12	2018 *n*=11
Between precipitation and										
rainy days	0.507 **	0.553 ***	0.866***	0.668 ***	0.530 ***	0.519 **	0.664 ***	0.936 ***	0.663 **	0.835 ***
number of nests	0.632 ***	0.051	-0.239	-0.152	0.092	-0.191	0.296	-0.452 *	-0.095	-0.181
clutch size	0.217	0.104	-0.411	0.264	-0.068	0.403 *	0.142	0.379	0.021	-0.376
Between rainy days and										
number of nests	-0.372	0.360 *	0.305	0.200	0.230	0.086	-0.110	0.388	0.530	0.084
clutch size	-0.017	-0.081	0.138	-0.080	-0.305	-0.632 ***	-0.122	-0.394	-0.093	0.088
Between number of nests and										
clutch size	-0.124	-0.024	-0.175	0.140	-0.296	0.273	0.170	0.288	0.057	-0.400

parameters (i.e., averages for each year's nesting season), which have fewer data points, rendered practically the same results as the trend calculated with the longer time series.

For both species, the start and duration of nesting season shifted later and shorter, respectively (Tables 1 and 2). For 2009-2018, long-term trends for leatherbacks showed a later start of the nesting season (First week with nests: correlation slope *b*= 0.90 weeks/year, r= 0.69, P ≤0.05) and a shorter nesting period (Season length: *b*= -0.85 weeks/year, *r*= -0.64, p ≤0.1). Similarly, for hawksbills, the nesting seasons shifted to later starts (*b*= 0.59 weeks/year, r= 0.73, P ≤0.05), and shorter durations (*b*= -0.76 weeks/year, *r*= 0.66, P ≤0.05). During the leatherback nesting period, which coincides with the dry season, there were no significant trends for any of the precipitation parameters. However, during the hawksbill nesting season, there was a long-term trend of fewer rainy days per week (*b*= -0.11 rainy days per week/year, r= -067 P ≤0.05).

DISCUSSION

General seasonal pattern for both species

There is a clear separation of the nesting season of leatherback and hawksbill sea turtles in the Gulf of Paria. Leatherbacks prefer to nest late in the dry season, allowing hatchlings to emerge during the rainy season. This is consistent with reports by Santidrian *et al.* (2015) regarding the greater number of leatherback newborns during increased precipitation conditions in areas with dry climates in four large rookeries worldwide. Conversely, hawksbills nest and emerge during the rainy period. The separation of nesting seasons between the two species could allow for the maximization of nesting on small rookeries such as ours.

Rainfall is deemed a positive factor for sea turtle reproduction (McGehee 1990, Bezy *et al.* 2016). However, for the period examined,

Table 5. (a) Partial correlations in a probability distribution of five variables: mean daily precipitation in a week, number of rainy days in a week, length of nesting season, number of nests per week, and average clutch size per week, in the Leatherback (*Dermochelys coriacea*) and the Hawksbill (*Eretmochelys imbricata*). The replicates are the mean values of each year. The values shown in the cells are the partial correlation coefficients. The asterisks indicate the level of significance of the two-tailed test; *P < 0.1, ** P < 0.05, *** P < 0.01. The values used for the calculations were the means of those of the weeks with nests; the number of these weeks is n. (b) Also shown are the simple correlations between some variables and year.

(a)

Partial correlations	**Leatherback n=9**	**Hawksbill n=10**
Between precipitation and		
rainy days	0.557	0.738 *
season length	-0.358	-0.370
number of nests	-0.005	-0.428
clutch size	0.470	-0.211
Between rainy days and		
season length	-0.024	0.298
number of nests	0.091	0.271
clutch size	0.023	0.471
Between Season length and		
number of nests	0.664	-0.637
clutch size	0.211	0.503
Between number of nests and		
clutch size	0.218	0.241

(b)

Correlations with year	**Leatherback n=9**	**Hawksbill n=10**
Avg. number nests	-0.459	0.313
Avg. clutch	-0.311	-0.875 ***
First week w/nests	0.691 **	0.731 **
Last week w/nests	0.057	-0.243
Season length	-0.643 *	-0.657 **
Number of weeks with nests	-0.763 **	-0.796 ***
Avg. prec. (nesting)	0.061	-0.131
Avg. prec. (seasonal)	-0.037	-0.113
Avg. rainy days (nesting)	0.256	-0.696 **
Avg. rainy days (seasonal)	-0.486	-0.692 **

precipitation showed no trends, and hawksbill fecundity decreased during the study period, possibly due to anthropogenic impacts (Balladares & Quintero-Torres 2019). Our results suggest that nest numbers depend more on human-related impacts and on biotic factors such as feeding and migration than on precipitation patterns.

Seasonal Correlations and Final remarks about Abiotic conditions vs. Fecundity of sea turtles in the region

Our analysis focused on the fecundity metrics nest numbers and clutch size. We did not consider hatching nor emergence success. Regarding this parameter, Olive Ridley turtles *Lepidochelys olivacea* in Costa Rica (Dornfeld *et al.* 2015; Bezy *et al.* 2016), had higher hatchling success during the rainy season than during the dry season. Rafferty *et al.* (2017) reported an increase in leatherback hatchling mortality with decreasing precipitation at Sandy Point National Wildlife Refuge (SPNWR). However, no such trend in local temperature or rainfall was observed between 1990-2010 at SPNWR, according to the same authors.

We did not find a statistically significant relationship between nest count and clutch size for either leatherbacks or hawksbills. If the number of nests is indicative of nesting females (Robinson *et al.* 2014), the absence of relation between nest count and size suggests that there is no density-dependence. Said differently, the density of mature females did not affect their fecundity in our study area. Halley *et al*. (2018) suggested that leatherbacks follow a Type III life history strategy of high fecundity, low juvenile survival, and increasing survival of later age classes, and the author concluded that organisms with this strategy are more strongly influenced by environmental variability and climatic changes. Halley *et al*. (2018) assumed a density-independent model for their study, suggesting that the role of density-dependence is still not well understood. In our case, while it is possible that density effects are present due to intraspecific competition, these are not expressed as a decrease in clutch size per female when density increases.

In the Gulf of Paria, the longest leatherback nesting season seen in 2009 was not related to precipitation variables but instead to a larger number of nesting females. Regarding hawksbills, during 2014 and 2010, significant correlations were found between clutch size and the number of rainy days per week. However, that relationship was not evident when analyzing the seasonal averages of all years together. Both parameters showed long-term trends of smaller clutch sizes and fewer rainy days per week. Although possible relationships between those two parameters are unclear, Balladares *et al*. (2020) found that larger hawksbill females in the region have more than twice the fecundity of younger reproductive females.

This work aimed to understand how precipitation, which in other regions regulates sea turtle nesting (Lolavar & Wyneken 2015, Bezy *et al.* 2016, Saragoça *et al.* 2020), affected the nesting of leatherback and hawksbill sea turtles in the southeastern Caribbean Sea. Aside from clear seasonality in both species, we could not demonstrate a clear relationship between variation or trends in precipitation and reproductive output during the study period (2009-2018). However, we did find that the nesting seasons for both leatherbacks and hawksbills are tending to start later and to be shorter. The drivers of these trends are worth exploring and could be related to other environmental variables (retaste temperatures or humidity inside the micro nesting environment), or to ecological factors such migrations, interspecific competition, feeding habits, or human activities.

It is important to sustain monitoring of the nesting characteristics of sea turtles to understand whether these patterns reflect short- or long-term changes associated with climate change (McGehee 1990, Hawkes et al 2009). However, though important to understanding climate impacts, long-term monitoring projects are challenging to maintain given limited resources, especially in less developed countries that provide critical habitats for endangered species such as sea turtles.

CONCLUSIONS

In the region of the Gulf of Paria in Venezuela, there is a clear time separation between the nesting seasons of leatherback and hawksbill sea turtles, with both seasons occurring during rainy months. During the study period (2009-2018) the nest count per year decreased in both species. Although in some years there seems to be some influence of precipitation on clutch size (leatherback) and on nests count and clutch size (hawksbill), the overall data indicate that precipitation does not influence these fecundity parameters in this region of the Southern Caribbean Sea.

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AUTHOR CONTRIBUTIONS

C.B.: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Writing - original draft.

D.R.R. and D.R.: Formal analysis; Methodology; Software; Supervision; Validation; Visualization; Writing - review & editing.

F.M.K and H.B.G.: Formal analysis; Supervision; Validation; Visualization; Writing - review & editing.

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