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Discovery of a Major East Pacific Green Turtle (*Chelonia mydas*) Nesting Population in Northwest Costa Rica

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ABSTRACT. – Here we report on a newly discovered nesting population of east Pacific green turtles (*Chelonia mydas*) in northwest Costa Rica at San José Island, Murciélagos Archipelago, that rivals those of Mexico and the Galápagos Islands, Ecuador. A total of 1232 individual green turtles were tagged over 4 nesting seasons (2012–2013 to 2015–2016). Mean (\pm SD) annual number of nests (1077 ± 414 ; range, 490–1698 nests) and females (306 ± 133 ; range, 164–466 females) was higher than those previously reported for Pacific Costa Rica. The number of deposited nests was similar to that registered on the Galápagos main beaches, but density of nests (number of nests/km) was the second highest for any green turtle beach in the eastern Pacific. Reproductive output was similar (mean clutch frequency: 4.4 ± 2.2 clutches and mean clutch size: 75.8 ± 14.6 eggs/clutch), and mean hatching success was higher (0.89 ± 0.14) than those reported at other sites in the eastern Pacific. Because the study site was located on an island within a protected area, several of the common threats that sea turtles face at more accessible mainland sites (i.e., egg poaching, tourist development, and predation by large mammals) were absent. Our data indicate that San José Island is the most important nesting site for east Pacific green turtles in Central America. The large size of this population, along with its isolated and protected status, suggest that this rookery is making a significant contribution to the conservation of east Pacific green turtles. Additional information at the country level will help determine the relative importance of Costa Rica for green turtle nesting in the broad eastern Pacific region.

KEY WORDS. – hatching success; east Pacific; reproductive output; island; sea turtle

The green turtle (*Chelonia mydas*) is listed as globally endangered on the IUCN Global Red List (International Union for Conservation of Nature 2017). In the eastern Pacific, this species is commonly known as the black turtle because of phenotypic differences with specimens from other geographic areas, such as the Indian and the Atlantic oceans, that are lighter in coloration (Cornelius 1982; Pritchard 1999). The green turtle populations of Pacific Central America are considered understudied because published records in scientific journals are scarce. In the eastern Pacific, the primary continental rookeries for this species are located in Michoacán, México (Alvarado-Díaz

et al. 2001; Delgado Trejo and Alvarado Díaz 2012); other important nesting grounds identified in the eastern Pacific region are found in the Galápagos Islands, Ecuador (Green 1984; Zárate et al. 2013) and the Revillagigedos Archipelago, Mexico (Holroyd and Trefry 2010).

Until recently there was little scientific information on east Pacific (EP) green turtles from Costa Rica with the exception of nesting activity described at the Santa Rosa National Park. In the 1970s, 80 females were recorded nesting at Naranjo beach and several aspects of their life history and nesting ecology were described (i.e., female size, reproductive output, nesting behavior, duration of the

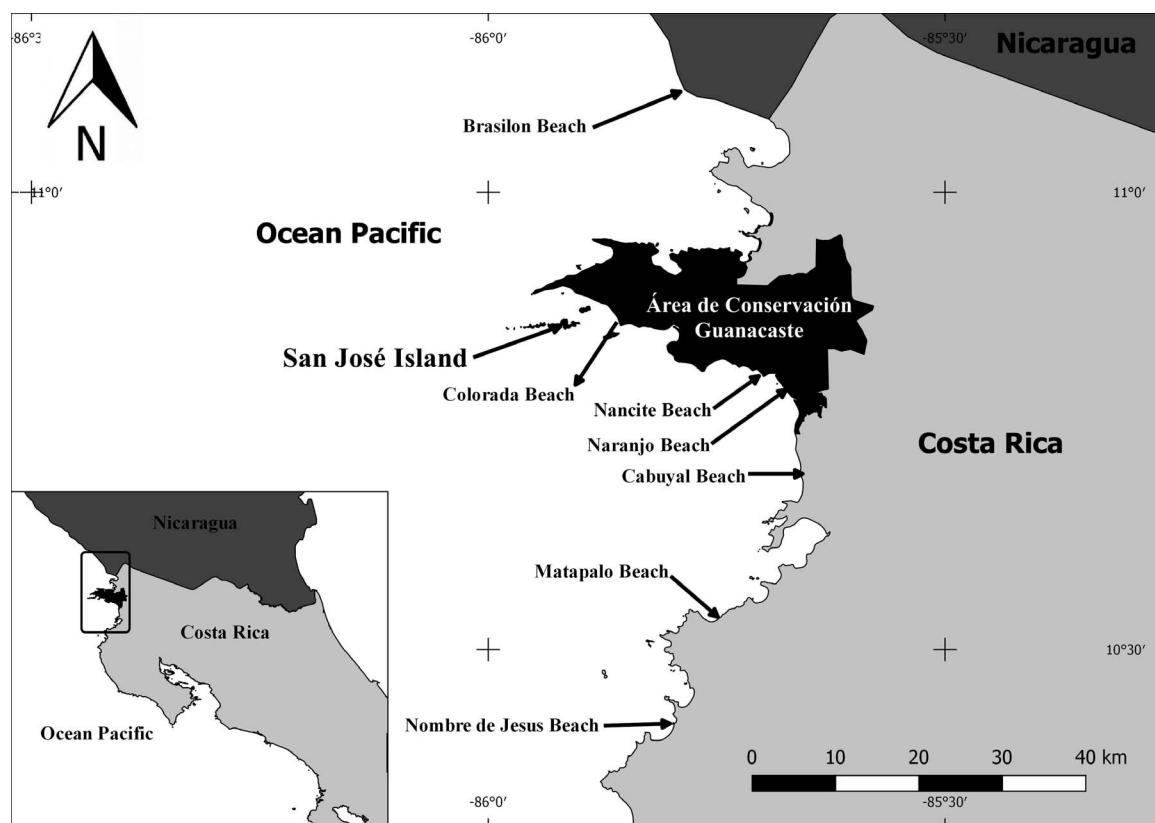


Figure 1. Map of San José Island in Guanacaste Conservation Area, Costa Rica, and nearby nesting beaches.

internesting period, and nesting phenology) (Cornelius 1976). In recent years, 3 additional nesting beaches have been found for EP green turtles in northwest Costa Rica: Cabuyal (Santidrián Tomillo et al. 2014), Matapalo (Urena Lopez 2014), and Nombre de Jesús (Blanco et al. 2012a; 2012b) (Fig. 1); and several aspects of green turtle biology were described for individuals from these sites.

Our main objective was to assess the importance of San José Island as nesting grounds for EP green turtles. Additionally, to improve our understanding of the biology of EP green turtles, we conducted an exhaustive analysis of the green turtles that nested here over 4 nesting seasons (2012–2013 to 2015–2016). Finally, we compared the nesting activity on the island with those registered in other areas of Costa Rica and of the EP and assessed its importance as a conservation site for the species in the region.

MATERIALS AND METHODS

Study Site. — San José Island is located in northwest Costa Rica ($10^{\circ}51'24.58''N$, $85^{\circ}54'45.07''W$) and is part of the Murciélagos Archipelago (Fig. 1), which is protected within the Área de Conservación Guanacaste (ACG), under the authority of the Ministry of the Environment. As mentioned above, the beach is largely free of anthropogenic threats because of the park's protection and the remoteness of the site. The waters surrounding the

archipelago are also protected by ACG, and activities such as fishing or extraction of marine life are not permitted, although enforcement is not robust. The nesting area is divided into 3 adjacent sections by rocky outcrops. The lengths of these sections from north to south are 80, 125, and 125 m. The edge of the vegetation of each section is populated mainly by saltgrass (*Distichlis spicata*), with a scarce presence of trees. The beach zone adjacent to the vegetation line is a sand dune, which is strongly modified by the wind.

Data Collection. — Trained field assistants (FAs) conducted daily surveys to determine nesting activity from October to late May over 4 nesting seasons: 2012–2013, 2013–2014, 2014–2015, and 2015–2016. Nightly patrols started at 1900 hrs and ended at 0400 hrs. Additionally, FAs monitored the beach every morning to count nesting tracks to confirm that we observed all turtles that visited the beach the previous night.

Every turtle encountered was inspected for tags. Turtles without tags were tagged with Inconel tags (model 681, National Band and Tag Company, Kentucky). Tagging procedure followed these general guidelines: 1) females were allowed to complete the egg laying process and tagging occurred as soon as nest covering began (except in those cases when females were tagged while returning to the ocean); 2) the scale was disinfected with a solution of vanodine prior to tag application; and 3) each turtle was tagged with one Inconel tag on the second

Table 1. Nesting phenology at the 3 main green sea turtle nesting beaches in the ETP. * = rainy season; X = peak nesting month.

Site	J	F	M	A	M	J	J	A	S	O	N	D
Mexico							*	*	*			
Costa Rica	X						*	*	*	X	X	X
Galápagos	X	X*	X*	*						*	X	X

proximal scale of each front flipper. After females had completed the egg laying process and were tagged, we measured the curved carapace length (CCL) notch to tip and curved carapace width (CCW) in centimeters with a flexible measuring tape (Bolten 1999). We determined clutch size at the time of exhumation.

We calculated the observed internesting period (OIP) from the number of days elapsed between 2 observed oviposition events by an individual female, as identified by her unique tag number. We excluded data where the interval was two times greater than the mode during the season, as this increases the likelihood that a turtle laid a clutch that was not observed (Reina et al. 2002). We calculated the estimated clutch frequency (ECF) for each turtle by dividing the number of days between her first and last observed nesting events by the mean OIP of the season and added 1 to account for the first nest (Santidrián Tomillo et al. 2014).

We marked nests with two 8-cm sections of 0.50-inch-diameter PVC tubes joined by 75-cm-long monofilament thread. One of the tubes was placed inside the nest chamber during oviposition, whereas the other was left outside the nest on the surface of the beach. The latter tube was labeled with the nest number and the oviposition date. We tied a plastic bottle to the tube at the surface to facilitate finding the clutch later, especially after high tides. To estimate clutch density, we divided the mean number of clutches per season by the length of the beach (km), following the methodology of Godley et al. (2001).

We excavated the contents of nests to determine hatching success 2 d after the last observed hatchling emergence or 55 d after oviposition. At excavation, we counted the number of shells, where more than 50% of a

broken shell was counted as an egg, and classified unhatched eggs into 4 developmental categories (Santidrián Tomillo et al. 2009). We estimated hatching success using the formula $H = S/(S + U)$, where S is number of hatched eggshells and U is number of unhatched eggs.

Statistical Analysis. — We used R Software v. 3.3.1 to conduct statistical analyses. We used 1-way analysis of variance (ANOVA) to compare differences between seasons in OIP and hatching success because the data were normally distributed. Statistical significance was assumed at $p \leq 0.05$.

RESULTS

Beaches in Costa Rica and Mexico generally showed evidence of similar turtle behavior, where peak nesting and rainy season took place about a month in advance in Colola relative to San José Island. In addition, peak nesting months at these 2 locations did not overlap with the rainy season. In contrast, the Galápagos rookeries exhibited a delayed peak in nesting months, which did overlap with rainy months (Table 1).

The average CCL was 85.4 cm ($n = 1209$, $SD = 5.9$ cm) and the average CCW was 81.2 cm ($n = 1209$, $SD = 4.2$ cm). Turtles deposited an average of 75.8 ± 14.6 eggs per clutch ($n = 2004$).

A total of 4308 green turtle egg clutches were recorded with an annual mean of 1077 clutches ($SD = 414$). The total number of clutches per season varied, ranging between 490 in 2015–2016 and 1698 in

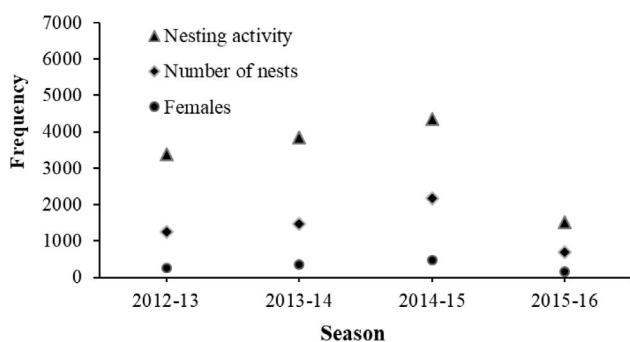


Figure 2. Nesting activity (successful plus nonsuccessful nesting), number of nests, and number of green turtle females registered per season (2012–2013 through 2015–2016) at San José Island, Costa Rica.

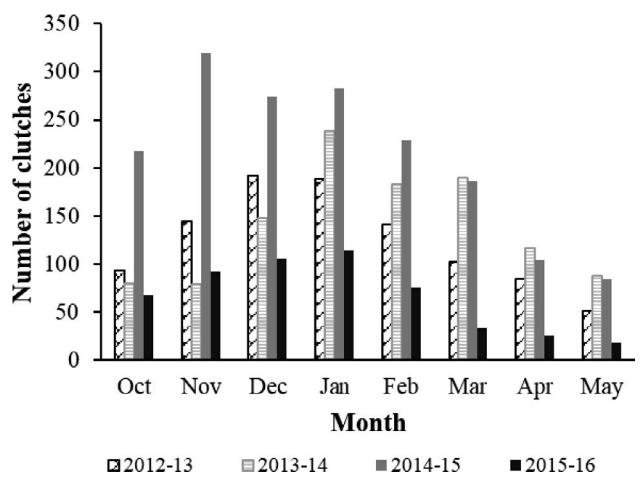


Figure 3. Distribution of number of green turtle (*Chelonia mydas*) nests at San José Island per month and season.

Table 2. Number (percent) of tagged green turtles (*Chelonia mydas*) that we encountered nesting in subsequent seasons on San José Island.

Season tagged	No. of females	Seasons		
		2013–2014	2014–2015	2015–2016
2012–2013	250	0 (0)	25 (10.0)	23 (9.2)
2013–2014	352	–	0 (0)	6 (2.0)
2014–2015	466	–	–	0 (0)
2015–2016	164	–	–	–

2014–2015 (Fig. 2). We observed year-round nesting with a distinct peak in January and the lowest level in May (Fig. 3). The highest number of clutches registered in a month was in November 2014–2015 (319 clutches), whereas the lowest recorded was in May 2015–2016 (18 clutches; Fig. 3). During the peak season (November–February), the mean number of turtles on the beach in a night was 5.8 turtles, and the highest number was 25 turtles.

We tagged a total of 1232 females. The mean number of tagged females per season was 306.2 (SD = 133.0) and ranged between 164 females in 2015–2016 and 466 females in 2014–2015 (Fig. 2). Some of the turtles marked in the first 2 yrs were recorded again in later years (Table 2). Of the females tagged in 2012–2013, 25% were recorded 2 yrs later in 2014–2015 and 9.2% 3 yrs later in 2015–2016. In addition, 6 females that nested in 2013–2014 also nested in 2015–2016 (Table 2). Turtles moved to nest between San José Island and nearby nesting beaches. Of the 1232 females identified at San José Island, 25 were also observed on nearby nesting beaches, all located within 52 km (Table 3). Most females exchanged nesting sites between Coloradas and San José Island ($n = 19$; 6 km away); the farthest location to exchange nesting females with San José Island was Nombre de Jesús ($n = 2$; 52 km away).

The maximum ECF was 11 clutches for 4 females during the 2013–2014 season. The mean OIP was 13.1 ± 2.3 d and was consistent among the different seasons (1-way ANOVA, $df = 3$, $F = 74.77$, $p > 0.05$).

We marked a total of 2180 egg clutches during this study (Table 4). Most of them were undisturbed during incubation (91.9%), 3.6% were eroded by wind, and 0.8% were excavated by other turtles. We were not able to find 3.7% of the clutches (Table 4). Overall mean hatching success was 0.89 ($n = 2005$, SD = 0.14). Mean annual hatching success ranged between 0.84 (in 2015–2016, $n = 195$) and 0.92 (in 2014–2015, $n = 381$) (Fig. 4). Over the duration of the study, a total of 282,335 hatchlings were produced. The annual production of hatchlings varied during the study period with the highest number (109,476 hatchlings) estimated in 2014–2015 and the lowest (30,127 hatchlings) in 2015–2016. We estimated that the clutch density for San José Island was 3264 clutches/km, which was second highest in the ETP region, based on published records (Table 5).

Table 3. Beach exchange of green turtle (*Chelonia mydas*) females tagged at San José Island that were recorded nesting at other beaches.

Beach	Country	No. of females	Distance (km)
Brasilon	Nicaragua	2	31
Coloradas	Costa Rica	19	6
Cabuyal	Costa Rica	1	33
Nancite	Costa Rica	1	23
Nombre de Jesús	Costa Rica	2	52

DISCUSSION

Importance of San José Island as Nesting Site for EP Green Turtles. — Our results showed that San José Island hosts the largest nesting aggregation of EP green turtles in Central America in terms of absolute numbers and appears to have the second highest clutch density of any nesting beach in the entire EP region. Within the EP, the green turtle population of Colola is considered the largest in the region and is increasing because of the near-complete cessation of illegal hunting at foraging grounds and reduction of egg poaching at nesting beaches (Alvarado-Díaz et al. 2001; Delgado Trejo and Alvarado Díaz 2012).

In Costa Rica, 4 nesting sites were previously identified along the Pacific Coast: Naranjo (Cornelius 1976; Drake et al. 2003), Cabuyal (Santidrián Tomillo et al. 2014), Matapalo (Urena Lopez 2014), and Nombre de Jesús (Blanco et al. 2012a, 2013b). All of these sites registered fewer than 300 clutches per year, which constitutes much lower levels than those of San José Island. Cabuyal Beach, where there has been a consistent monitoring effort since 2011–2012 (Santidrián Tomillo et al. 2014), accounts for $\sim 25\%$ of the mean number of turtles identified at San José Island in a given year.

Despite the presence of park rangers since 1996, there are no historical or anecdotal records of sea turtle nesting activity at San José Island. The best recollection of nesting activity by park rangers is the nesting of 3 or 4 turtles per night. Before park rangers were present, the island was used as a refuge by local fishers who poached turtle eggs. Thus, protection of this beach over the past 20 yrs, and possibly low poaching levels before then, may have contributed to the currently high nesting abundance.

Nesting Ecology. — The nesting season coincides with that of leatherback turtles (*Dermochelys coriacea*) in the EP (October–February) (Reina et al. 2002; Sarti Martínez et al. 2007). The nesting season at San José Island mainly occurs between November and February, and the peak season between January and February, with January being the peak month when all 4 seasons were taken into account. However, there was some variability in the nesting peak among years by up to 2 mo. For example, November and December registered the most nesting in 2014–2015 and 2012–2013, respectively. This temporal nesting pattern was previously documented at Cabuyal, where the nesting peak varied by 1 mo between years

Table 4. Survival of marked green turtle (*Chelonia mydas*) clutches at San José Island for the period between 2012–2013 and 2015–2016.

Clutch survival	2012–2013	2013–2014	2014–2015	2015–2016
Completed development (%)	93.9	90.7	89.9	94.2
Eroded by wind	13	33	28	4
Excavated by other turtles	5	7	4	1
Lost	29	33	12	7
Total no.	765	783	425	207

(Santidrián Tomillo et al. 2014). The nesting peak in the area coincides with the end of the rainy season and with the beginning of the north winds, which induce a significant decrease in sea surface temperature as a result of upwelling in the area (Jímenez 2001). Perhaps the number of nesting turtles is regulated in some fashion by local environmental conditions, such as winds and sea surface temperature.

Nesting phenology of green turtles differed somewhat among the 3 main nesting beaches in the EP. In general, peak nesting months in Galápagos rookeries occur after those of rookeries in the northern hemisphere. In addition, the Galápagos green turtle peak nesting months overlapped with peak rainy months, unlike the rookeries in Costa Rica and Mexico. These patterns suggest that the nesting phenology of EP green turtles is likely influenced by local climatic conditions, leading the season to begin earlier in the north and later in the south.

Some (11.7%) of the San José Island green turtles returned to nest after 2 seasons and 9.2% after 3 seasons, but it is too soon to know what the dominant remigration intervals are for this population. At Colola Beach, which has maintained a tagging program for over 2 decades, the great majority of the turtles had a remigration interval of 3 or 4 yrs (Delgado-Trejo 2016); in the Galápagos Archipelago, the majority of turtles had a remigration interval of 4 or 5 yrs (Zárate 2009). A longer record is required to elucidate the actual situation at San José Island

because remigration rates may vary according to climate changes such as the El Niño Southern Oscillation (ENSO), the warm phase of which has been linked to a reduction in primary productivity and an increase in the remigration interval (Limpus and Nicholls 1988; Wallace and Saba 2009).

As expected, because of geographic proximity and the observed migration of green turtles from Galápagos to Costa Rican foraging areas (Seminoff and Shanker, 2008), female size (CCL) at San José Island (85.4 cm) seemed similar to that of Cabuyal (86.2 cm) and the Galápagos Archipelago (85.0 cm) and to those of Colola Beach (83.1 cm). Similarly, clutch size at Colola (~ 67 eggs), Cabuyal and San José (both 76 eggs), and the Galápagos (73 eggs) (Zárate 2002, 2009; Santidrián Tomillo et al. 2014), was similar. Thus, female and clutch sizes fall well within the sizes of EP green turtles that are generally smaller than those of other populations in the world, such as the green turtles that nest in the Caribbean, where green turtles can exceed 104 cm (Reyes and Troëng 2002) and lay over 100 eggs per clutch (Fowler 1979).

OIP fluctuated between 12 and 14 d, being slightly shorter than the 15.4 d recorded at Cabuyal (Santidrián Tomillo et al. 2014). Because OIP is affected by sea surface temperature (Hays et al. 2001), differences in mean OIP between Cabuyal and San José may reflect differences between nesting seasons rather than differences between sites. Likewise, fluctuations in OIP have also been observed among seasons in Colola and the Galápagos Archipelago, where OIP oscillated between 13 and 16 d (Zárate 2002, 2004, 2009; Alvarado-Díaz et al. 2003). Strong northeast winds are typical in the months of December and January in Costa Rica; the winds normally cause generalized upwelling in the region, leading to a significant reduction in sea surface temperatures (Jímenez 2001). This low temperature regime likely influences OIP in the later months, increasing its length because of an expected reduction in metabolic rate. In fact, longer OIPs were registered later in the season in Cabuyal (Santidrián Tomillo et al. 2014).

Estimated clutch frequency was high and similar to that reported for Cabuyal (4.4 vs. 4.3 clutches; Santidrián Tomillo et al. 2014) and higher than that exhibited by the turtles of Colola (3.1 clutches; Alvarado-Díaz et al. 2003). This difference may be explained by the high monitoring effort that we maintained on this beach and the high nest-

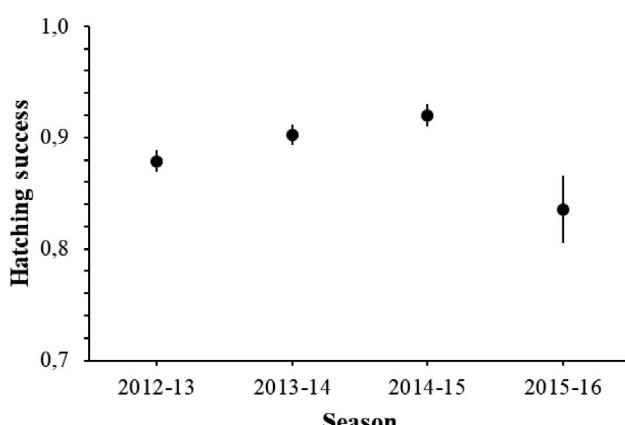


Figure 4. Mean hatching success of green turtle (*Chelonia mydas*) nests per season at San José Island from 2012–2013 through 2015–2016.

Table 5. Description of the main nesting sites of the east Pacific green turtle (*Chelonia mydas*).

Beach	Country	Length (km)	Mean no. of nests	Nests/km	Source
Colola	Mexico	4.8	22,789	4748	Delgado-Trejo 2016
Quinta Playa	Ecuador	2.0	1467	734	Zárate 2002, 2004, 2009
Bahía Barahona	Ecuador	1.2	754	629	Zárate 2002, 2004, 2009
San José Island	Costa Rica	0.3	1077	3264	This study

site fidelity that turtles exhibited. Because of the small size of the nesting area (350 m), the great majority of nesting females were seen, and only 2% of the females were found to nest on other beaches, although it is likely that some turtles nested on beaches that were not monitored actively.

Hatching success and clutch survival were high at San José Island, likely leading to a higher production of hatchlings than those at other sites. The anthropogenic pressures that reduce sea turtle reproductive output along the continental coast such as egg poaching (Santidrián Tomillo et al. 2014), urban development (Urena Lopez 2014), and predation by jaguars, coyotes, and raccoons (Drake et al. 2003; Alvarado et al. 2016) are nonexistent at San José, increasing clutch survival. Additionally, hatching success was high and consistent with that reported at other green turtle rookeries, such as Colola (Delgado Trejo and Alvarado Díaz 2012), Tortuguero (Fowler 1979), Cyprus (Broderick and Godfrey 1996), and Taiwan (Cheng et al. 2009) (all greater than 80%), and higher than that of the Galápagos, which was < 50% because of predation by beetles and feral pigs (Zárate et al. 2013).

There was some destruction of clutches by other females, but the rate of destroyed clutches was lower than expected (0.8%) for a 350-m beach. Because turtles showed some preference to nest near the vegetation or under trees, the available nesting space was greater than that provided by just the beach area. This preference was reported at Cabuyal (Santidrián Tomillo et al. 2014), where clutches under the vegetation represented a higher proportion than those located at the edge of the vegetation. Another factor that reduced the probability of clutch destruction by a turtle was the presence of a sand dune with a surface of approximately 1500 m². This dune has an elevation of more than 7 m at its highest point relative to sea level, and turtles were seen nesting up and down the dune. The presence of the dune increased the surface area of the beach.

We estimated that 282,335 hatchlings were produced at San José Island over 4 yrs, which was proportional to the number of clutches laid during the study period. Production was lowest during the 2015–2016 season, when we recorded the lowest number of nesting turtles and lowest hatching success. This low hatching success coincided with a warm El Niño event. Such El Niño events are thought to reduce precipitation and increase air temperature in the area, which increases embryonic and hatchling mortality in sea turtle clutches (Santidrián

Tomillo et al. 2012). However, for reasons not understood, the effect of El Niño on egg mortality was not as pronounced in green turtles as in the leatherback (Santidrián Tomillo et al. 2012) and olive ridley (*Lepidochelys olivacea*) turtles (Valverde et al. 2010).

As mentioned above, San José Island seems to be the main nesting site for EP green turtles in Central America, but there are several nearby beaches along the continental coast of Costa Rica where EP green turtles also nest. If we add the numbers of turtles nesting at Coloradas, Nancite, Naranjo, Cabuyal, Matapalo, Nombre de Jesús, and the beaches of difficult access of the Papagayo Peninsula, at least 500 females could nest every year in northwest Costa Rica. This number implies that this region is at least as important for EP green turtles as the beaches of Mexico and the Galápagos. The high nesting and high hatchling productivity at San José Island suggest that passive management (i.e., minimal or no interference with the natural reproduction of the species in the area) is appropriate for the conservation of green turtles here because there are not significant anthropogenic threats or natural predators at this location. However, the impact of incidental fishing and degradation of foraging habitats should also be evaluated, which may threaten San José Island and other nesting populations in the area.

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