

## Local Variation in the Interesting Behavior of Green Turtles in the Gulf of Papagayo, Costa Rica

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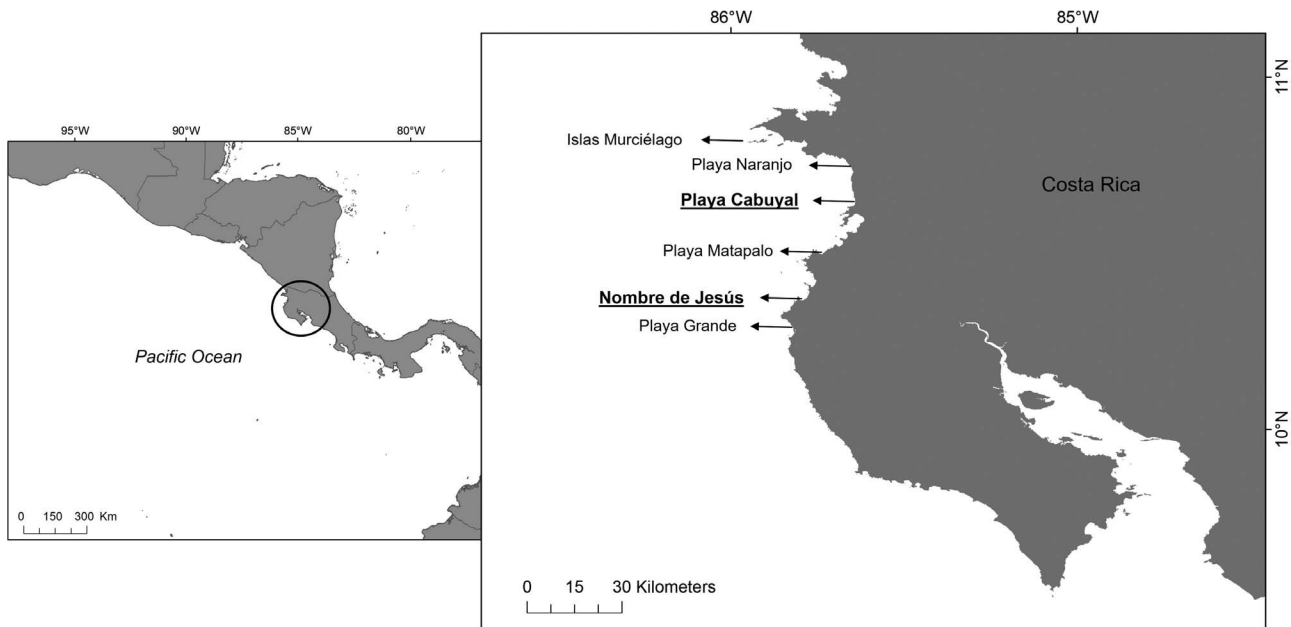
**ABSTRACT.** – Marine turtles often conduct extensive migrations from foraging to breeding habitats. Turtles may spend several months in these breeding habitats, while periodically taking brief excursions onto terrestrial environments to nest. Identification and protection of these breeding habitats over the duration of the reproductive season is therefore vital for the conservation of sea turtles. Here, we used satellite telemetry to investigate the interesting behavior of East Pacific green turtles from 2 nesting beaches: Nombre de Jesús and Playa Cabuyal, located 50 km apart on the Pacific coast of Costa Rica. A total of 21 satellite transmitters were deployed at Nombre de Jesús ( $n = 8$ ) between 2007 and 2009 and at Cabuyal ( $n = 13$ ) between 2012 and 2015. We found that turtle movements and dive behaviors were notably different between the 2 beaches. Specifically, the turtles from Cabuyal engaged in deeper dives ( $10 \pm 3$  m vs.  $6.5 \pm 2$  m [mean  $\pm$  SD]), presumably because they had access to deeper waters, and had larger minimum convex polygon area ( $606.5 \pm 1150.5$  km<sup>2</sup> vs.  $16 \pm 11$  km<sup>2</sup>) than turtles from Nombre De Jesús. Turtles from Nombre de Jesús also engaged in shorter dives ( $6.68 \pm 4.5$  min), compared with Cabuyal, where a majority of dives lasted between 10 and 30 min ( $18.75 \pm 5.6$  min). Finally, turtles at Nombre de Jesús dove significantly deeper during the day compared with the night, a pattern that was not present at Cabuyal. We conclude that interesting behaviors can be different even between beaches within the same geographical area. As such, interesting habitat management plans should pay specific attention to potential site-specific variation in interesting behaviors.

**KEY WORDS.** – diving behavior; eastern Pacific; Gulf of Papagayo; *Chelonia mydas*; interesting; northwestern Costa Rica

Green turtles (*Chelonia mydas*) are listed as endangered (International Union for Conservation of Nature 2004). In the eastern Pacific, green turtles face a wide range of threats related to low and unpredictable resource availability and anthropogenic pressures, such as habitat loss and both direct and incidental mortality (Alvarado-Díaz et al. 2001; Hays et al. 2003; Seminoff 2004; Fischer and Wolff 2006; Koch et al. 2006; Dapp et al. 2013; Senko et al. 2014). Many initiatives have addressed nest poaching and established conservation programs on nesting beaches (e.g., Alvarado-Díaz et al. 2001; Santidrián Tomillo et al. 2015); however, protecting only one part of their life cycle is not, in itself, sufficient to support population recovery in sea turtles (Crouse et al. 1987; Plotkin 1995). Addressing in-water threats requires knowledge of species' spatiotemporal distribution, specifically critical habitats, home

ranges, migration corridors, and identification of parameters that influence their distribution (Hamann et al. 2010).

The area used by green turtles between nesting events can vary markedly between populations around the world. In some cases, turtles remained close to the nesting beach during interesting intervals (Mediterranean: Schofield et al. 2010; Costa Rica: Blanco et al. 2013; Indian Ocean: Richardson et al. 2013). Conversely, some turtles moved away from nesting beaches between subsequent nesting events within a season (Caribbean: Carr et al. 1974; Atlantic Ocean: Mortimer and Portier 1989; Indian Ocean: Richardson et al. 2013). These data suggest that habitat use reflects available habitats; further, individuals nesting on a single nesting beach display individual habitat use patterns and combinations of restricted area use and movement patterns between nests (Richardson et al. 2013; Esteban et



**Figure 1.** Map of Playa Nombre de Jesús, Cabuyal, and surrounding green turtle (*Chelonia mydas*) nesting beaches in North Pacific Costa Rica, adapted from Santidrián Tomillo et al. (2015).

al. 2015). Despite variable area use, turtles often maintained comparable rates of movement during the interesting interval (Carr et al. 1974; Blanco et al. 2013; Chambault et al. 2016).

Differences in dive behavior are also present during the interesting interval. For example, green turtles in Pacific Costa Rica generally dive to 10-m depths or less, spending most of their time resting, either at the surface or performing U-shaped dives (Blanco et al. 2013), characterized by a direct descent down to a constant depth, followed by a direct ascent to the surface. Similarly, green turtles around Ascension Island spend the interesting interval diving to depths closer to 10 m (presumably to rest due to the lack of sea grass pastures) and only surface for brief intervals (31% of time; Hays et al. 2002b). In contrast, green turtles from Cyprus spend most of the interesting interval (90%) at shallow depths (< 4 m), with mean depths close to 3 m, and remain close to shore foraging on seagrass (Hochscheid et al. 1999; Hays et al. 2002b). Coastal waters are very important for interesting green turtles and interesting behavior can differ between locations. Considering the existence of multiple nesting beaches for green turtles along the Pacific coast of Costa Rica, area-specific studies are essential for implementation of effective conservation strategies.

Current data on nesting East Pacific green turtles in Pacific Costa Rica suggest that there are several nesting beaches along the Pacific coast (Cornelius 1976, 1995; Blanco et al. 2012, 2013; López 2014; Santidrián Tomillo et al. 2015). During the nesting season in Costa Rica, green turtles lay  $\sim 4$  clutches per season at  $\sim 15$ -d intervals (Santidrián Tomillo et al. 2015); however, beach patrols might overestimate nesting population numbers (Esteban et al. 2017). The purpose of this study was to

build on a previously published study investigating interesting behavior in East Pacific green turtles nesting on Nombre de Jesús, Costa Rica (Blanco et al. 2013) by comparing data from that study to interesting behaviors of East Pacific green turtles nesting on Cabuyal, Costa Rica. We analyzed the movement patterns and dive behaviors of these 2 populations of turtles to describe the range of behaviors seen in Pacific Costa Rica. Comparative studies of sea turtles from 2 beaches along the same coast within the same ocean provides insights into the general interesting behavior of turtles. Further, understanding beach-specific turtle behaviors and habitat use is vital for effective conservation plans for East Pacific green turtles in one of the most important nesting regions for this species in the eastern Pacific.

## METHODS

*Study Sites.* — Our study builds on previous work investigating the interesting movements and behavior of East Pacific green turtles nesting on Nombre de Jesús ( $10^{\circ}24'N$ ,  $85^{\circ}48'W$ ) by reanalyzing the raw data from that study and comparing it to new data collected at a second beach, Cabuyal ( $10^{\circ}42'N$ ,  $85^{\circ}48'W$ ), Costa Rica (Blanco et al. 2013). These 2 study sites are located on the Guanacaste Peninsula of Costa Rica separated by  $\sim 50$  km. Nombre de Jesús and Cabuyal are sandy beaches 1 and 1.4 km in length, respectively (Fig. 1). Nesting season for green turtles on these beaches extends from August until April, although some scattered nesting may occur year-round (Cornelius 1995). At Nombre de Jesús, we did not have complete beach coverage, so we cannot estimate total nesting population size (Blanco et al. 2013). At Cabuyal, there is an ongoing project that manages beach

patrol from August through April every year with estimated between 63% and 87% beach coverage (Santidrián Tomillo et al. 2015). From 2010 to 2013, 181 turtles were encountered, with an observed clutch frequency of  $3.3 \pm 2.0$  clutches ( $n = 120$ ) and a total of 298 marked nests (Santidrián Tomillo et al. 2015). Recorded East Pacific green turtle nesting also takes place on Playa Grande to the south of Nombre de Jesús; Matapalo, located between Nombre de Jesús and Cabuyal; and Naranjo and Islas Murciélago to the north (Fig. 1).

The study by Blanco et al. (2013) took place between the months of August and March in the years 2007 and 2009, while our new data were collected between August and March in 2012, 2013, 2014, and 2015, during which time we patrolled beaches at night. When we encountered turtles after they successfully nested, we assessed the reproductive state of their ovaries with a portable ultrasound (Aloka SSD-500; Hitachi Aloka Medical, Ltd, Tokyo, Japan). If a turtle still had vitellogenic follicles, we concluded she would nest again and attached the satellite transmitter (Blanco et al. 2012). We measured curved carapace length and width, and recorded observed interesting period (OIP). Finally, we tagged each turtle with a unique passive integrated transponder (PIT) (AVID FriendChip Identification Systems Inc, Norco, CA) injected into the right anterior flipper.

*Satellite Transmitters.* — Over the course of 6 different seasons, we tracked and monitored the interesting movements of 21 individual green turtles. At Nombre de Jesús, we equipped 8 turtles with satellite transmitters (Mk10; Wildlife Computers Inc, Redmond, WA) between August 2007 and November 2009 (see Blanco et al. 2013). Farther north, at Cabuyal, an additional 8 turtles were equipped with carapace-mounted transmitters (SPOT5; Wildlife Computers Inc), and 5 with tethered transmitters (Mk10) between 2012 and 2015. The SPOT5 transmitters provided location data; the MK10 transmitters were tethered pop-up archival tags that recorded location, depth, temperature, and light level data, from which dive behavior was inferred. We attached the SPOT5 transmitters following the method of Balazs et al. (1996) modified by Seminoff et al. (2008). We attached Mk10 transmitters using a tethering method following Morreale et al. (1996) modified by Robinson et al. (2016). We collected data on multiple OIPs for 8 turtles; however, we only included the first recorded interval in these analyses to maintain consistency with other 13 turtles for which we recorded a single interesting interval.

*Movement Analysis.* — Location data were relayed via the ARGOS satellite system. We filtered locations using a speed filter (R statistical software, R 3.3.0, Vienna, Austria) which removed any point that required a travel speed  $> 5$  km/hr as we assumed that those positions were not realistic (Luschi et al. 1998); we then selected the best location per day to account for cloud cover bias. We calculated a fixed kernel density analysis using ArcGIS 10.2 (Esri, Redlands, CA). To carry out the analysis we

used filtered locations for turtles pooled together by nesting beach weighted by individual. Core areas were determined by the 25%, 50%, and 95% utilization distribution area. In order to compare individual movements, we calculated the area used by each turtle using minimum convex polygons (MCPs) using the Geospatial Modelling Environment for ArcGIS (<http://www.spatial ecology.com/gme/>). Further, we compared individual MCP area between beaches using a Kruskal-Wallis rank sum test. We calculated track length for each individual and daily travel distance using the “argosfilter” package for R (R 3.3.0) for all but 1 turtle from Cabuyal, for which the transmitter only relayed 7 of the 13 d of location data. In addition, we overlaid filtered locations for each turtle from both beaches with bathymetry maps (General Bathymetry Chart of the Oceans, [www.gebco.net](http://www.gebco.net)) to determine water depth in which turtles were spending their interesting intervals.

*Dive Analysis.* — We programmed pop-up tags to register dives greater than 2 m to avoid false positives from wave action and swimming along the surface. We downloaded summary dive data from processing centers; further, we downloaded dive data directly from transmitters that we recovered from turtles. We programmed transmitters to record summary dive depth data into bins of 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, and 70 m and dive duration data into bins of 2, 5, 10, 15, 20, 30, 40, 45, 50, 60, 75, 90, 120, and 120+ min, averaged over 6-hr periods: 0000–0600, 0600–1200, 1200–1800, and 1800–0000 hrs. Because of satellite transmitter failure, we collected data for 7 turtles from Nombre de Jesús and 5 from Cabuyal for dive depth, and for dive duration, we had 2 turtles from Nombre de Jesús and 5 turtles from Cabuyal. We recovered 7 transmitters from the turtles, but 14 transmitters remained on the turtles. When we recovered MK10 transmitters from a turtle, we downloaded fine-scale (1 data point/sec) dive depth and duration data from the transmitter. We used the Wildlife Computer Instrument Helper (version 3.0.447 26-Apr-2017, Redmond, WA) to analyze turtle dives.

*Statistics.* — We reanalyzed raw data collected by Blanco et al. (2013) and compared it with newly collected data from turtles nesting at Cabuyal (this study). For both data sets, we conducted univariate analyses of covariance tests (ANCOVAs), comparing interesting interval (d), total travel distance (km), daily travel distance (km), mean depth (m), and mean duration (min) between beaches (using year as a covariate) and between years (using beach as a covariate); when data did not meet assumptions, we used Kruskal-Wallis mean rank tests ( $\chi^2$ ). We compared retrieved transmitter dive depth between day (0600–1800 hrs) and night (1800–0600 hrs) using a paired samples *t*-test. Next, we combined mean dive data and mean depth data and ran a Kruskal-Wallis mean rank test to determine if dive depth was correlated with duration (the data did not meet the assumptions for a parametric test). We used linear regression analyses to determine whether OIP varied with

**Table 1.** Interesting parameters of East Pacific green turtles (*Chelonia mydas*) nesting in Nombre de Jesús (NJ) and Cabuyal (CAB). Results are from univariate analysis of covariance with beach and year either being the independent variable or covariate. Values are mean  $\pm$  SD, with ranges in parentheses. For track length, one turtle from CAB was removed owing to the transmitter only recording 7 of 13 d of location points. For dive depth, CAB  $n = 5$  and NJ  $n = 7$ ; for dive duration, CAB  $n = 5$ , NJ  $n = 2$ . OIP = mean observed interesting period; CCL = curved carapace length; CCW = curved carapace width; \* = significant differences. Data from NJ were reanalyzed from Blanco et al. (2013).

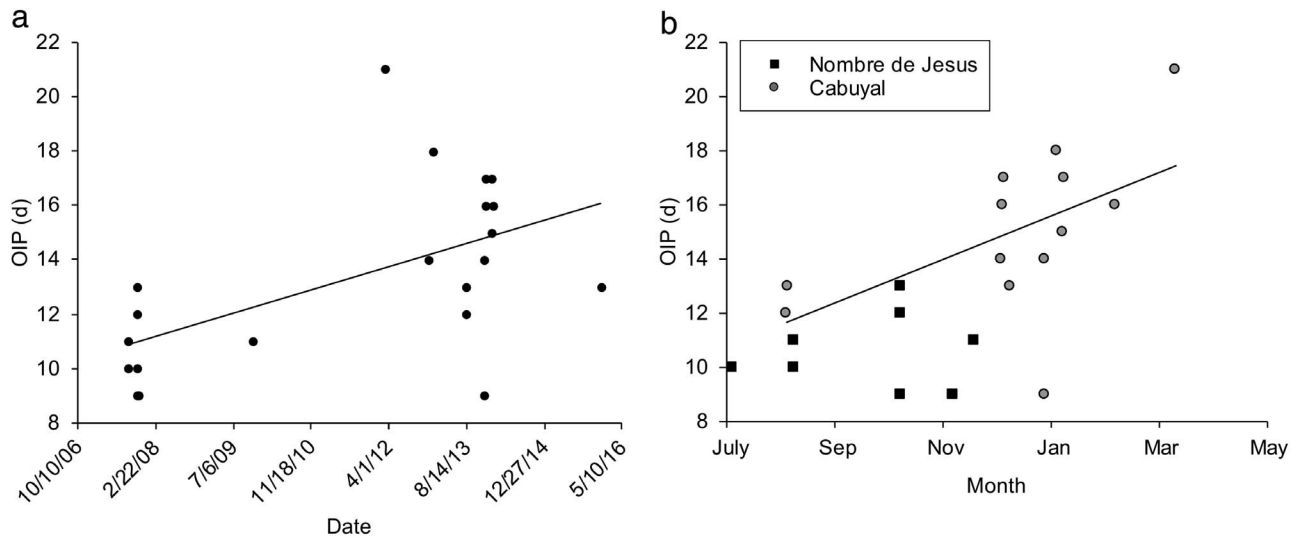
|                                       | Sample size ( $n$ ) | OIP (d)               | Total distance traveled (km)                         | Daily distance traveled (km/day)                     | Mean dive depth (m)                                  | Mean dive duration (min)                          | CCL (cm)     | CCW (cm)   |
|---------------------------------------|---------------------|-----------------------|--|--|--|---|--------------|------------|
| NJ                                    | 8                   | 10.6 $\pm$ 1.4 (8–15) | 33 $\pm$ 13 (11–48)                                  | 3 $\pm$ 2 (1–5)                                      | 6 $\pm$ 3 (3–10)                                     | 7 $\pm$ 0.05 (3–10)                               | 85 $\pm$ 2.5 | 81 $\pm$ 3 |
| CAB                                   | 13                  | 15 $\pm$ 3.1 (11–21)  | 140 $\pm$ 120 (27–486)                               | 9 $\pm$ 6 (2–23)                                     | 11 $\pm$ 7 (5–16)                                    | 19 $\pm$ 3.7 (11–27)                              | 85 $\pm$ 2.5 | 79 $\pm$ 3 |
| ANCOVA results by beach               |                     |                       | $F_{1,17} = 7.284, p = 0.015^*$ , $\eta_p^2 = 0.300$ | $F_{1,17} = 8.556, p = 0.009^*$ , $\eta_p^2 = 0.335$ | $F_{1,9} = 10.513, p = 0.010^*$ , $\eta_p^2 = 0.539$ | $F_{1,4} = 2.754, p = 0.172$ , $\eta_p^2 = 0.408$ |              |            |
| ANCOVA/Kruskal-Wallis results by Year |                     |                       | $\chi^2_4 = 10.402, p = 0.034^*$                     | $\chi^2_4 = 9.841, p = 0.043^*$                      | $F_{3,7} = 2.504, p = 0.143$ , $\eta_p^2 = 0.518$    | $F_{3,2} = 2.416, p = 0.302$ , $\eta_p^2 = 0.787$ |              |            |

month of the season and year. We performed all statistical analyses using SPSS 24 (IBM SPSS Statistics for Windows, Version 24.0, IBM Corp, Armonk, NY) and R statistical software (Version 3.4.4). We accepted a statistical significance of  $p < 0.05$ , and we present results as mean  $\pm$  standard deviation (SD).

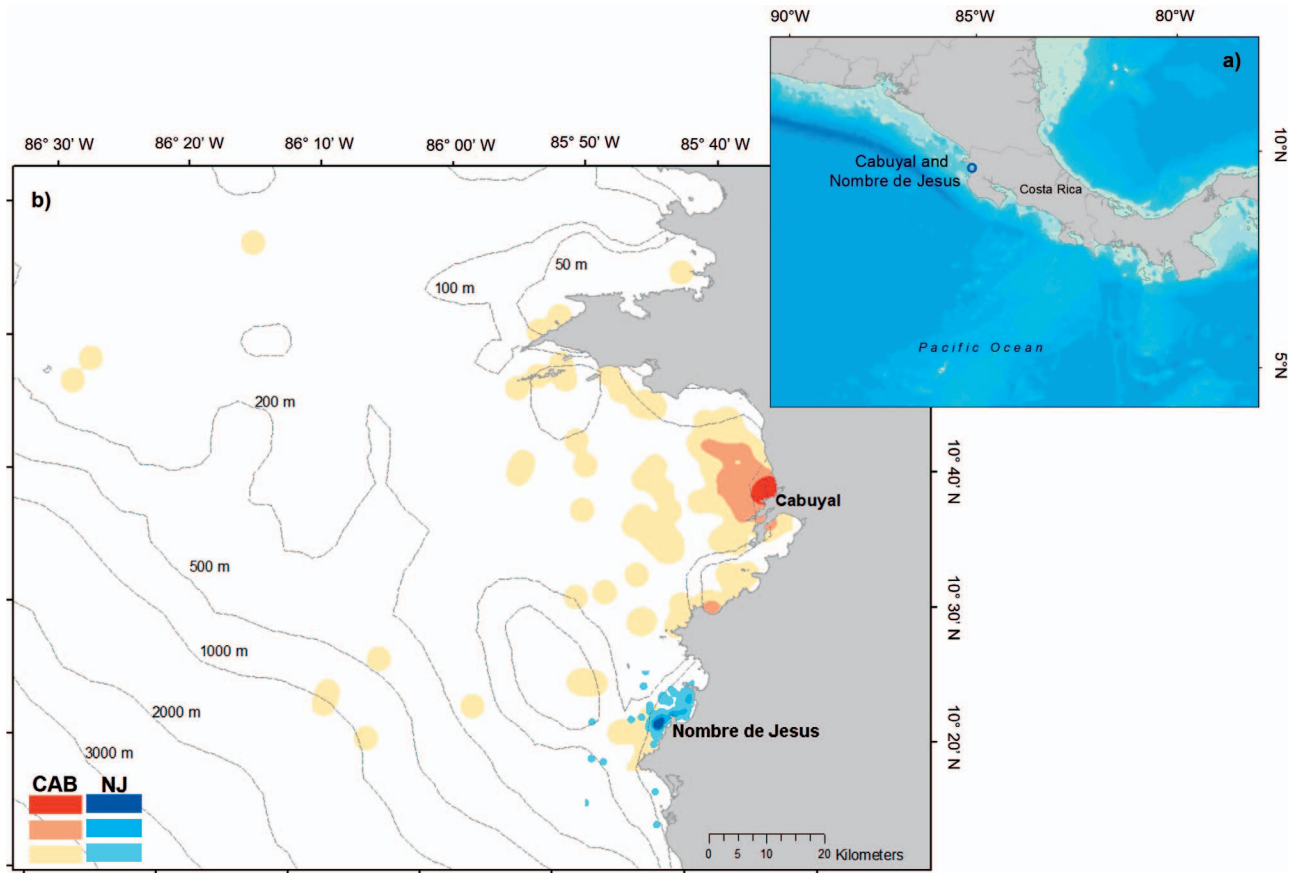
## RESULTS

We reanalyzed and compared location data from Nombre de Jesús collected from 8 individuals in 2007 and 2009 (Blanco et al. 2013) and newly collected data from Cabuyal on 13 individuals in 2012, 2013, 2014, and 2015, totaling 280 d of transmission (Table 1). For 7 turtles from Nombre de Jesús (Blanco et al. 2013) and 5 turtles from Cabuyal, we also retrieved dive data. Over the course of the study, Blanco et al. (2013) was able to retrieve 4 transmitters from turtles at Nombre de Jesús and we retrieved 3 transmitters from individuals at Cabuyal. Altogether, interesting intervals ranged from 8 to 21 d. We found that when we graphed OIP in days, against date, there was a weak positive relationship between the two ( $R^2 = 0.241$ ,  $F_{1,19} = 6.036$ ,  $p = 0.024$ ; Fig. 2), and when we graphed OIP against months into the nesting season, we identified no relationship for turtles from Nombre de Jesús ( $R^2 = 0$ ,  $F_{1,6} = 0$ ,  $p = 0.998$ ) and a positive linear relationship for turtles from Cabuyal ( $R^2 = 0.369$ ,  $F_{1,11} = 6.424$ ,  $p = 0.028$ ; Fig. 3).

**Movement Analysis.** — Track length (the cumulative calculated distance between daily location points) ranged between 10 and 485 km for all turtles during their interesting intervals. Between nesting events, turtles from Nombre de Jesús traveled between 10 and 50 km ( $33 \pm 13$  km), while turtles from Cabuyal traveled significantly farther with distances varying between 27 and 485 km ( $140 \pm 120$  km; Table 1). Daily travel distances ranged between 3 and 15 km, with turtles from Nombre de Jesús ( $3 \pm 2$  km) traveling significantly less than turtles from Cabuyal ( $9 \pm 6$  km; Table 1). Travel times across years were significantly different (Table 1). Shorter travel distance was related to smaller area use at Nombre de Jesús compared with Cabuyal (Fig. 3b). Kernel density analyses demonstrated that 95% of the locations for interesting turtles at Nombre de Jesús occurred within 39.7 km<sup>2</sup>, while the 95% area use for Cabuyal was 671 km<sup>2</sup>. Turtles from Nombre de Jesús remained within 5 km of the nesting beach, except 1 turtle that traveled 23 km south, remaining within 4 km of the coastline. Most turtles from Cabuyal remained within 25 km from the beach, and 2 turtles traveled north and south (121 and 71 km, respectively) between nesting events. Results from individual MCPs revealed wide range in area within turtles from each beach (Table 2; Figs. 4 and 5), and significantly different area use between beaches ( $\chi^2_1 = 8.804$ ,  $p = 0.003$ ). Specifically, turtles nesting on Nombre de Jesús displayed reduced area use ( $16 \pm 11$



**Figure 2.** Observed interesting period (OIP), in days, against (a) date and (b) month of the nesting season. (a) All data from Nombre de Jesús (2007–2008, 2009–2010) and Cabuyal (2011–2012, 2012–2013, 2013–2014, 2015–2016) were pooled together with the date on the *x* axis indicating the start of the OIP.  $R^2 = 0.241$ ,  $p = 0.024$ . (b) Data from Nombre de Jesús (2007–2008, 2009–2010) and Cabuyal (2011–2012, 2012–2013, 2013–2014, 2015–2016) were graphed separately. Nombre de Jesús:  $R^2 = 0$ ,  $p = 0.998$ . Cabuyal:  $R^2 = 0.369$ ,  $p = 0.028$ . Data from Nombre de Jesús were reanalyzed from Blanco et al. (2013).



**Figure 3.** (a) Study area and (b) kernel density analysis of interesting locations from East Pacific green turtles (*Chelonia mydas*) nesting in Cabuyal (CAB) and Nombre de Jesús (NJ). Dark to light colors represent 25%, 50%, and 90% kernel boundaries. Data from NJ were reanalyzed from Blanco et al. (2013).

**Table 2.** Individual dive depth, duration, and area use (MCP) for each green turtle (*Chelonia mydas*) sampled in this study. Deployment date indicates month and year transmitters were deployed. Dive depth and duration are presented as mean  $\pm$  SD. MCP = minimum convex polygons; NJ = Nombre de Jesús; CAB = Cabuyal; — = no data. Data from NJ were reanalyzed from Blanco et al. (2013).

| Deployment date | Turtle  | Beach | Mean depth (m)    | Mean duration (min) | MCP area (km <sup>2</sup> ) |
|-----------------|---------|-------|-------------------|---------------------|-----------------------------|
| Aug 2007        | 11528   | NJ    | 5.26 $\pm$ 3.43   | —                   | 9.20                        |
| Aug 2007        | 11509   | NJ    | 3.42 $\pm$ 1.61   | 3.17 $\pm$ 2.67     | 1.70                        |
| Oct 2007        | 37803   | NJ    | 6.83 $\pm$ 1.92   | —                   | 20.30                       |
| Oct 2007        | 37799   | NJ    | 6.12 $\pm$ 2.86   | —                   | 34.40                       |
| Oct 2007        | 37795   | NJ    | 4.29 $\pm$ 1.27   | —                   | 21.00                       |
| Oct 2007        | 37794   | NJ    | 9.74 $\pm$ 3.24   | —                   | 25.70                       |
| Nov 2007        | 37800   | NJ    | —                 | —                   | 17.30                       |
| Nov 2009        | 3780009 | NJ    | 3.92 $\pm$ 1.29   | 10.31 $\pm$ 2.6     | 12.60                       |
| Mar 2012        | ANA     | CAB   | —                 | —                   | 4196.2                      |
| Dec 2012        | 1078931 | CAB   | —                 | —                   | 290.3                       |
| Jan 2013        | 1078932 | CAB   | —                 | —                   | 573.3                       |
| Aug 2013        | 1078933 | CAB   | —                 | —                   | 74.5                        |
| Aug 2013        | 107897  | CAB   | —                 | —                   | 707.8                       |
| Dec 2013        | 107882  | CAB   | 11.84 $\pm$ 10.79 | 22.96 $\pm$ 11.83   | 170.7                       |
| Dec 2013        | 107884  | CAB   | 13.22 $\pm$ 8.25  | 18.61 $\pm$ 7.3     | 393.5                       |
| Dec 2013        | 1078811 | CAB   | 15.97 $\pm$ 9.0   | 27.55 $\pm$ 15.38   | 202.4                       |
| Dec 2013        | 1078934 | CAB   | —                 | —                   | 409.1                       |
| Jan 2014        | 107898  | CAB   | —                 | —                   | 9.9                         |
| Jan 2014        | 107899  | CAB   | —                 | —                   | 11.7                        |
| Feb 2014        | 1078812 | CAB   | 8.43 $\pm$ 3.67   | 14.56 $\pm$ 10.14   | 239.4                       |
| Dec 2015        | 107903  | CAB   | 5.43 $\pm$ 1.62   | 11.70 $\pm$ 6.02    | —                           |

km<sup>2</sup>) compared with turtles nesting on Cabuyal (606.5  $\pm$  1150.5 km<sup>2</sup>).

**Dive Behavior.** — Taken together, the turtles in this study showed a slight bimodal distribution in binned dive depths, with the 0–5-m and the 16–20-m bins having the highest percentage of dives (Fig. 6a). Dive depth data from Nombre de Jesús demonstrated that 58% of dives were within the top 5 m of the water column, and 86% of dives were within 10 m of the surface, while 33% of dives from Cabuyal occurred within the top 5 m of the water column and 77% of dives were within 10 m of the surface (Fig. 6a). We found that mean dive depth was significantly shallower for interesting turtles at Nombre de Jesús (6.5  $\pm$  2 m) than for turtles from Cabuyal (10  $\pm$  3 m; Table 1). Turtles from Nombre de Jesús used areas with depths ranging from 2 to 100 m (19  $\pm$  19.3 m), while turtles from Cabuyal spent their interesting period in waters from 2 to 575 m depth (62  $\pm$  73.5 m). Variation in dive depth suggests that the 5 turtles from Cabuyal and 7 turtles from Nombre de Jesús used shallower bins inconsistently, but deeper bins were used in similar frequencies (Table 2; Fig. 6a); however, turtles from Nombre de Jesús did not use water deeper than 45 m, while turtles from Cabuyal dove as deep as 100 m.

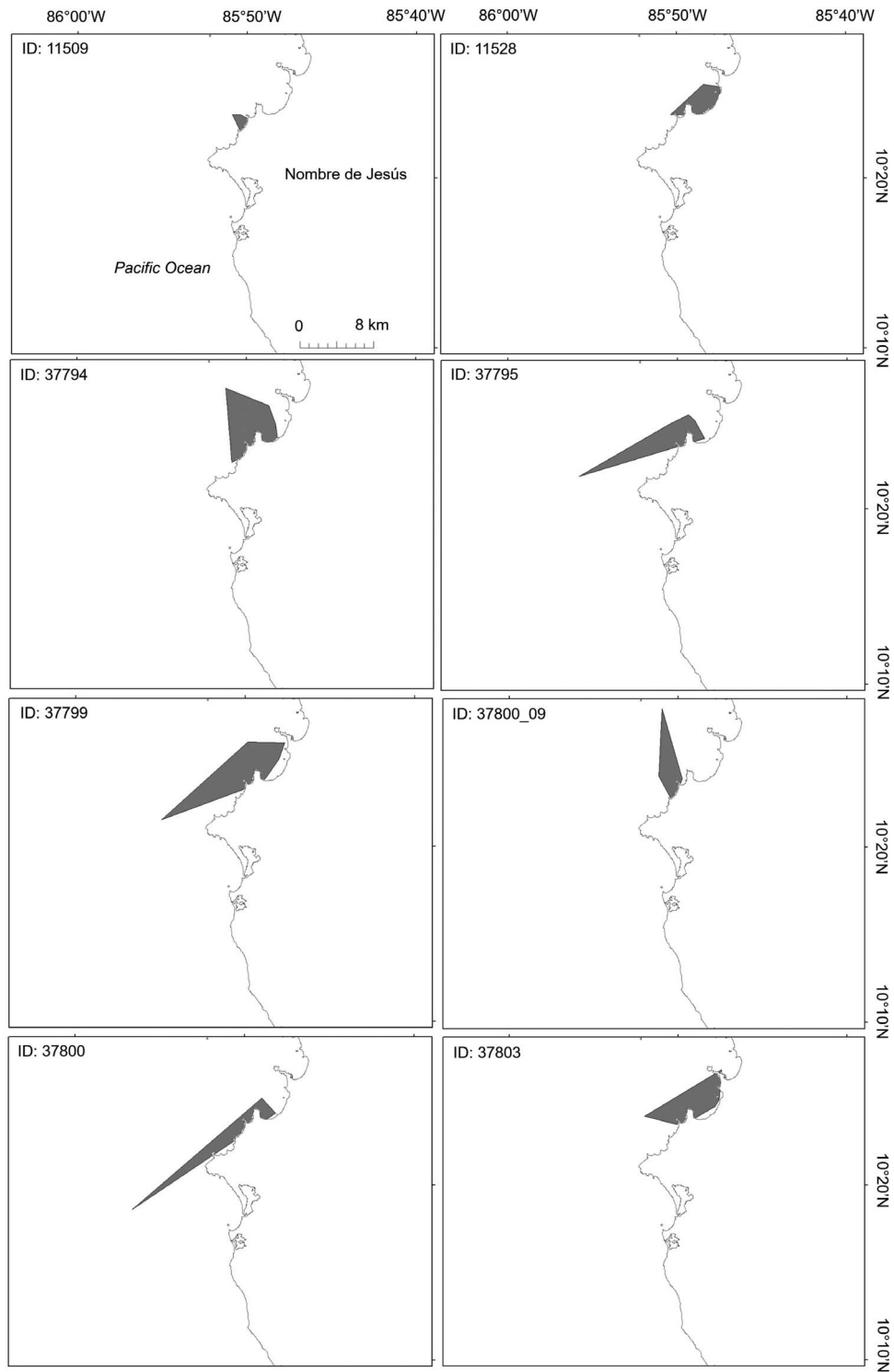
Dive durations were shorter at Nombre de Jesús (6.68  $\pm$  4.5 min) than at Cabuyal (18.75  $\pm$  5.6 min), where the highest percentage of dives lasted between 10 and 30 min (Fig. 6b). At Nombre de Jesús, 39% of the dives were shorter than 2 min, and 99% of dives were shorter than 30 min, while at Cabuyal 9% of the dives were shorter than 2 min, and 89% of dives were shorter than 30 min. As such, turtles from Nombre de Jesús had a higher percentage of dives within the collective 30-min bins than Cabuyal (ANOVA,  $F_{1,7} = 6.496$ ,  $p = 0.051$ ; Fig.

6b). Variation in duration demonstrated that 5 turtles from Cabuyal and 2 turtles from Nombre de Jesús used shorter dive bins in individually unique frequencies; however, turtles from Nombre de Jesús never used longer dive bins (longer than 50 min), while turtles from Cabuyal all used them similarly (Table 2; Fig. 6b). When data from both beaches were combined, dive depth was not correlated to dive duration ( $\chi^2_5 = 5.893$ ,  $p = 0.317$ ).

Turtles at both beaches engaged in between 725 and 6101 dives during the OIP, with deepest depths reaching 93+ m and longest dives lasting 45+ min (data from retrieved transmitters). For 3 turtles nesting on Cabuyal, dives during the day (0600–1800 hrs) were deeper than during the night (1800–0600 hrs), but these results were not significant (paired sample  $t$ -test,  $p = 0.157$ ). Turtles from Nombre de Jesús spent significantly more time at the surface during the night than during the day (ANOVA,  $p < 0.0001$ ; Blanco et al. 2013).

## DISCUSSION

Breeding habitats are important for conservation of sea turtle populations, and previous studies suggest that turtles nesting throughout the world show different behaviors during this time. Here, we show that these site-specific behaviors are also present at nesting beaches within the same area. We analyzed movement and dive behavior between turtles nesting in Cabuyal and Nombre de Jesús, beaches that are only  $\sim$  50 km apart, and assess how these differences may imply a need for differential management strategies. Data from this study demonstrated that although all East Pacific green turtles in this study spent the interesting interval within the vicinity of the nesting beach, dove to the 6- to 10-m bin depth (on average), and engaged in dives shorter than 20 min (on



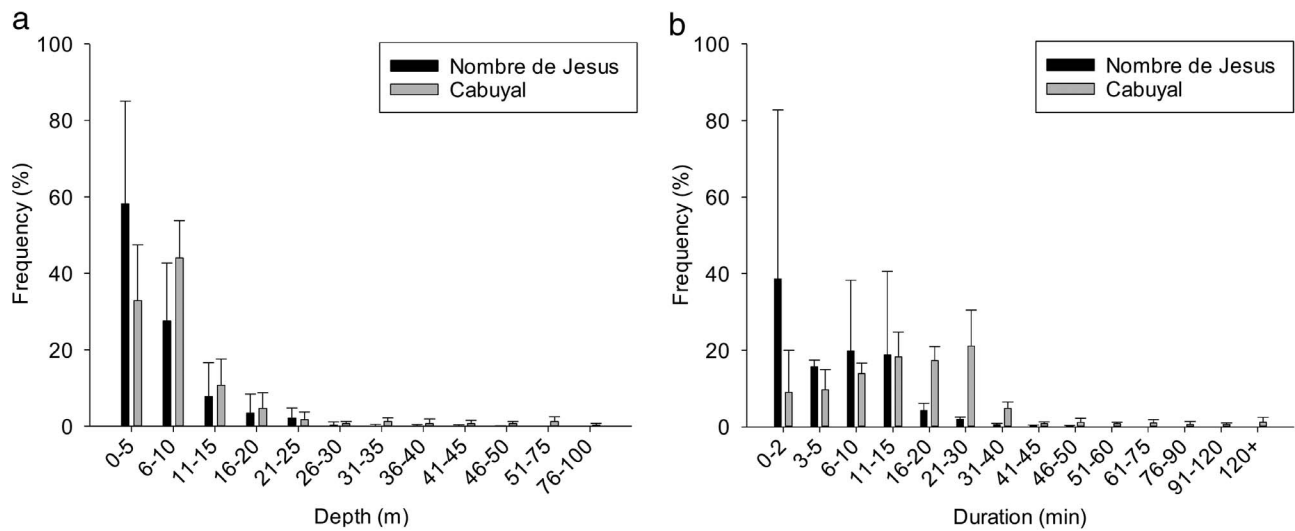
**Figure 4.** Individual minimum convex polygons (MCPs) in km<sup>2</sup> of interesting turtles tagged at Nombre de Jesús (2007–2008, 2009–2010). Data were reanalyzed from Blanco et al. (2013).

average), turtles from Cabuyal had significantly larger area use, traveled significantly farther, and dove significantly deeper than turtles from Nombre de Jesús (Blanco et al. 2013). As such, our data support the conclusion that site-specific behaviors are important to the implementation of conservation and management plans, even when beaches are close to each other and turtles belong to the same

genetic stock. This study took place across 6 yrs, which exposed turtles from both nesting beaches to various oceanic conditions. Without comparing both Nombre de Jesús and Cabuyal concurrently, it is difficult to infer whether differences in behavior were due specifically to beach differences or other factors such as variability of environmental conditions within and between years (e.g.,



**Figure 5.** Individual minimum convex polygons (MCPs) in km<sup>2</sup> of interesting turtles tagged at Cabuyal (2011–2012, 2012–2013, 2013–2014, 2015–2016).



**Figure 6.** (a) Mean dive depth (SD; Cabuyal [CAB],  $n = 5$  and Nombre de Jesús [NJ],  $n = 7$ ) and (b) mean dive duration (SD; CAB,  $n = 5$ ; NJ,  $n = 2$ ) of East Pacific green turtles (*Chelonia mydas*) during the interesting interval at CAB and NJ (Blanco et al. 2013) nesting beaches. Satellite-linked data were summarized into (a) 12 binned depths or (b) 13 binned time lengths. Data from NJ were reanalyzed from Blanco et al. (2013).



el Niño conditions, differences in interannual currents, temperature, austral summer upwellings, and nutrient availability; Jiménez 2002; Alfaro and Cortés 2012; Amador et al. 2016). We believe examining multiple years and beaches strengthens our generalizations about behavior and helps the development of management strategies for our study area.

We observed a wide range of interesting interval length in this study (8–21 d). Although 21 d is longer than the standard reported interesting interval for green turtles (~ 14 d), this study is not the first study to record OIP of this length (up to 25 d; Sato et al. 1998; Valverde-Cantillo et al. 2019). Within this study, as the season progressed, the OIP lengthened, corroborating existing literature on temperature and nesting intervals (Sato et al. 1998; Hays et al. 2002a; Santidrián Tomillo et al. 2015; Valverde-Cantillo et al. 2019). In Guanacaste, between December and March, surface water temperatures are colder (as low as 24°C) than earlier in the nesting season (August; up to 28°C) (<https://seatemperature.info/>). Sato et al. (1998) recorded sea turtle body temperature to be consistently 1°–2°C above water temperature in green and loggerhead sea turtles (*Caretta caretta*;  $n = 15$  and  $n = 2$ , respectively); when body temperature drops to ~ 23°C (water temperature ~ 22°C), 21 d are needed for vitellogenesis (Weber et al. 2011). Additionally, if water temperatures adjacent to nesting beaches were cold, female turtles would need to use activity to maintain a body temperature sufficient for egg development, potentially depleting energy stores at a faster rate (Fossette et al. 2012).

Temperature in the eastern Pacific is subjected to dynamic effects of El Niño Southern Oscillations (ENSO), where El Niño events coincide with warmer water temperatures and reduced upwelling (lower nutrient availability); La Niña events result in colder water temperatures, with normal conditions (Oceanic Niño Index [ONI] between -0.5 and 0.5) in between (National Oceanic and Atmospheric Administration 2017). We found a slight increase in OIP over time in this study (from 2007 to 2015). During our sampling dates at Nombre de Jesús, 2007–2008 was a strong La Niña year (ONI between -1.9 and -1.5) while 2009–2010 was a moderate El Niño year (ONI between 1.0 and 1.4). At Cabuyal, our 21-d OIP turtle nested at the end (March) of a moderate La Niña year (ONI between -1.4 and -1.0), while the majority of the turtles nested during normal ONI years (2012–2013, 2013–2014), and the final turtle nested during a very strong El Niño cycle (2015: ONI  $\geq 2.0$ ). The combination of timing during the nesting season and ONI explains the variability seen in OIP in this study, and clarifies recorded significance in OIP between beaches. It is important to consider annual variation in temperature and its recorded effects on the behavior parameters measured (Sato et al. 1998; Hays et al. 2002a, 2002b; Schofield et al. 2010).

Turtles sampled from both beaches demonstrated a high degree of nest site fidelity, nesting almost exclusively

on the beaches where they were tagged. However, some level of exchange has been observed between East Pacific nesting beaches (indicated by flipper tag and genetic studies), suggesting turtles in this region belong to the same larger population (Dutton et al. 2014; Hart et al. 2015). Moreover, long-distance migration studies revealed turtles from distinctly different foraging areas converge to nest at the Costa Rican beaches. For example, Blanco et al. (2012) recorded turtles nesting on Nombre de Jesús that migrated to feeding areas as far south as Panama and north to Honduras. During sampling on Cabuyal, we did not encounter any turtles previously tagged with PIT tags from Nombre de Jesús, indicating that each turtle used in this study only nested on the beach listed. However, not all turtles are tagged with PIT tags, and flipper tags applied to the front flippers of green turtles are subject to high loss rates (Heidemeyer et al. 2018). Outside the dates of this study, we cannot definitively determine whether Cabuyal and Nombre de Jesús have overlap in nesting females, although it is possible because of the proximity of beaches (Fig. 1).

*Movement Analysis.* — We observed beach-specific track lengths and area use in turtles sampled in this study. However, all turtles used nearshore habitats with turtles from Nombre de Jesús confining their movements to the coastline to a greater degree than turtles from Cabuyal. Even within these trends, individual variability in interesting area use was present at both beaches. Use of a smaller area around Nombre de Jesús is consistent with that observed for green turtles in the Caribbean (Hart et al. 2013, 2017), the Atlantic around French Guiana (Chambault et al. 2016), the Mediterranean (Schofield et al. 2010), and the Indian Ocean (Richardson et al. 2013). However, in some cases, area use was influenced by year, a pattern that could explain some of the individual variability in our study (Schofield et al. 2010). Further, of studies where turtles remained close to the nesting beach during the interesting interval, the very restricted area use observed in turtles from Nombre de Jesús was unique (Richardson et al. 2013; Chambault et al. 2016). Large area use, similar to what we observed at Cabuyal, is more common and has been reported for green turtles throughout the world (Carr et al. 1974; Mortimer and Portier 1989; Meylan 1995; Richardson et al. 2013). Further, in the Caribbean and at Ascension Island, turtles engage in a combination of behaviors, where they travel away from the nesting beach, followed by small home ranges in specific interesting habitats (Carr et al. 1974; Esteban et al. 2015). In our study, turtles remained adjacent to nesting beaches, suggesting that turtles were not migrating to resting habitats. Rather, it suggests that all necessary habitats exist within close proximity of nesting beaches, which potentially reduces energy expenditure associated with nesting seasons. Additionally, all turtles moved slowly, further supporting energy conservation and suitability of coastal habitats for interesting turtles.

In the Caribbean, green turtles confine interesting habitat to areas with seagrass beds located adjacent to deeper water; however, the reason for this habitat selectivity is likely due to the bathymetry constraints more so than foraging opportunities (Hart et al. 2013). Access to deep water may provide favorable resting habitats reducing energetic costs during nesting seasons (Jiunn 2009). Difference in area use (this study) may be the result of different available habitats determined by coastal landforms such as coves and gulfs along the shoreline (e.g., Richardson et al. 2013). Cabuyal is located in the Gulf of Papagayo, which provides more protection from higher-energy waves and currents than habitats along Nombre de Jesús, where turtles must remain close to shore to avoid open ocean currents (Figs. 4 and 5). The behavior of nesting turtles in this study supports an increasing body of work that highlights the need for flexible management strategies that prioritize marine protection adjacent to nesting beaches (Hart et al. 2013, 2017).

*Dive Behavior.* — At both beaches, turtles engaged in shallow dives that lasted less than 10 min. Dive behavior, or vertical movement, can be linked to horizontal movement in sea turtles. For example, shallow dives are often used when turtles are migrating (Hays et al. 1999; Hochscheid et al. 1999; Rice and Balazs 2008). However, this is not the case in this study as the turtles engaging in shallower dives had smaller areas of use. Most dives in this study were shorter than 30 min and shallower than 50 m, which is consistent for green turtles across their range and is also found in other hard-shelled turtle species (Hochscheid et al. 1999; Tucker and Read 2001; Houghton et al. 2002; Hamel et al. 2008; Howell et al. 2010; Liles et al. 2015). Hochscheid et al. (2010) suggested that a turtle will surface often and remain at the surface in order to recover from anaerobic dives; however this is not the case here, as turtles maintained short dive times.

Differences in dive behavior could be explained by the availability of offshore habitats present at Cabuyal, allowing turtles a wider range of potential depth selection, while turtles from Nombre de Jesús are limited to surface or shallower depths. Further, individual variation in dive duration and depth demonstrates that although overall patterns are beach specific, individuals at each beach were not uniform in their use of depth or duration bins. Specifically, shorter and shallower bins resulted in individual dive frequencies (Table 2; Fig. 6a–b). Dive behavioral differences could be explained by the availability of offshore habitats present at Cabuyal, allowing turtles a wider range of potential depth selection, while turtles from Nombre de Jesús were limited to surface or shallower depths. For example, traveling directly off the coast of Cabuyal, turtles reach depths of 50 m approximately 8 km from the shore, and maximum depths of 100 m at 10.5 km from the beach, whereas turtles from Nombre de Jesús travel 4 km from the shore before reaching their maximum depth (Blanco et al. 2013) of 50 m (<https://www.google.com/earth/>). These observations

are supported by retrieved transmitter data in this study. For example, while turtles from Nombre de Jesús exhibited shallow, short dives, they dove deeper during the day and spent night hours resting at the surface. This suggests that turtles in these waters do not have access to desired resting depths below the surface. In contrast, turtles from Cabuyal did not show dive differences between day and night, indicating a wider range of depth availability from which turtles could select. Although depth use in sea turtles can be a result of lung capacity and depth at which sea turtles are neutrally buoyant, the turtles in this study were comparable in size and therefore have similar buoyancy in water (Minamikawa et al. 1997).

In many parts of the world, turtles have been observed resting during the interesting interval to conserve energy while fasting and preparing a subsequent clutch of eggs, which is metabolically expensive (Hamann et al. 2002; Wallace et al. 2005; Hart et al. 2013). Resting behaviors take place along the ocean bottom, at the surface, at levels where they experience neutral buoyancy (19 m), or in areas where they are sheltered from water current systems (Minamikawa et al. 1997; Hays et al. 2000, 2002a; Houghton et al. 2002; Seminoff et al. 2006; Howell et al. 2010; Blanco et al. 2012, 2013; Hart et al. 2013). Area use from turtles at Cabuyal include areas deep enough to select varying depths to rest, while turtles at Nombre de Jesús might have to struggle to remain on the shallow ocean floor and instead rest at the surface. Turtles diving to the ocean floor could be using these dives as resting dives but also as foraging dives, and without complete dive profiles it is difficult to tease out what dive types are being used.

Although the standard sea turtle reproductive model assumes that females fast for migrations and nesting intervals, green turtles in the Mediterranean and Australia spent the nesting season foraging on available sea grass (Hochscheid et al. 1999; Tucker and Read 2001; Hays et al. 2002a). There are scattered foraging opportunities along the north coast of Costa Rica, in addition there are algae communities and invertebrates (Amorocho and Reina 2007; Bernecker and Wehrmann 2009; Quiñones et al. 2010). A majority of the turtles from Nombre de Jesús nested during La Niña years, suggesting normal primary productivity years and food availability, as opposed to El Niño years, which lack comparable levels of food availability. Turtles from Cabuyal nested during normal ENSO years, where there was significantly more primary productivity. Taken together, the depth of dives from turtles in this study could suggest opportunistic foraging, although ENSO exerts its environmental influence prior to the nesting season, not during it.

ENSO patterns alter sea surface temperature, and as traditionally non-endothermic animals, sea turtles maintain body temperature by moving in and out of thermal zones (Davenport 1997; Minamikawa et al. 1997; Chambault et al. 2016). Thermoregulation is important in the development of subsequent clutches of eggs, and the presence of warm and cold water pockets allows turtles to select those

that aid in controlling body temperature and supporting reproduction (Sato et al. 1998; Hays et al. 2002a; Southwood et al. 2005; Wallace et al. 2005; Hazel et al. 2009). When water temperature is colder (low 20s Celsius) turtles engage in shallower, shorter dives compared with months when water temperature is warmer (high 20s Celsius; Southwood et al. 2003). However, as stated above, the coldest sea surface temperatures in this area during our sampling window was closer to 24°C (<https://seatemperature.info/>). Additionally, at Nombre de Jesús, most of the turtles nested during an El Niño year, signified by warmer water temperatures, but used shallower depths, suggesting shallower, shorter dives were not due to basking to maintain warmer body temperature.

While shallower recorded dive depths could be linked to mating behavior, it is generally thought that sea turtles mate before nesting ensues and avoid mating again to avoid the energetic cost (Phillips et al. 2014; Schofield et al. 2017). However, at Cabuyal, volunteers have seen pairs of turtles at the surface, suggesting some of the short, shallow dives here could be due to mating behavior. Another reason turtles dive is to avoid predation, and while this is not relevant to sea turtles nesting at Nombre de Jesús due to their proximity to the coast and inhabitation of shallow water, it could explain some of the individual deep dives recorded from Cabuyal (Lutcavage and Lutz 1997). Although we have observed sharks in the water adjacent to Cabuyal, we have not observed interactions between turtles and sharks or turtles displaying signs of interaction with sharks. Lastly, we did not retrieve sufficient data to investigate dive depth or duration across the duration of the nesting season.

In conclusion, turtles from Nombre de Jesús use surface water more frequently and deeper depths less frequently than turtles from Cabuyal, and as such engage in shorter dives. The most likely reasons for these differences in behavior are the depth of the ocean near Cabuyal, and the use of these deeper waters for resting, foraging, or predator avoidance. Individual variation in dive behavior could suggest potential mating, predator avoidance, or foraging or resting preference. However, in general a preference for water shallower than 30 m and dives shorter than 30 min was consistent across beaches and years. The travel distance and subsequent area use by turtles reflects the shape of the coastline where the Gulf of Papagayo provides a wider reservoir for Cabuyal into which the turtles move.

### Conservation Implications

To be successful, conservation management plans must consider all the threats that endangered animals face at all stages of their life cycle. During breeding seasons, sea turtles congregate for several months in nearshore habitats while nesting. Here, we demonstrated that even though there are many similarities in turtle behavior across the globe, differences can be observed in sea turtle

behavior even between nearby nesting beaches. The observed differences in diving and surfacing behavior, and differences in core area use between beaches underscores the need for site-specific management plans when determining how to best protect interesting sea turtles. Similar studies are warranted across a broader region if generalized and effective management plans are to be developed. Although the status of East Pacific green turtles has not been regionally assessed, if threats are not abated, these populations could easily decline in the future, especially in an area with heavy fishing pressures and high levels of anthropogenic impact and development; as such, intervention is crucial before significant population-level impacts can take hold (Wallace et al. 2011).

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