INTRODUCTION

Despite a growing interest in the effects of climate change on sea turtle populations, few studies have assessed those produced by certain beach features, such as scarp slopes, that arise as a result of erosion. Coastal dune systems are dynamic and are affected by sand erosion–accretion cycles, which determine coastal topography and affect the quality of sea turtle nesting habitats (Eckert 1987, Mazaris et al. 2009). One of the consequences of beach erosion is the increased presence of dune scarps (Morton & Sallenger 2003), which are defined as “features with a slope larger than the critical angle of repose of 32° and a
minimum height of 0.25 m’ (Soulsby 1997). Beach erosion influences the morphological changes that beach scarps undergo and, generally, reduces beach height, width, and quality of beaches (Donnelly 2007). A scarp’s persistence depends on wave overtopping events during high water levels and wave heights during storms (Jackson et al. 2010, de Alegría-Arzaburu et al. 2013). Additionally, sea-level rise induces long-term erosion on sandy beaches (Bruun 1962, Dickson et al. 2007, Dawson et al. 2009), with the rate of this erosion considered to be about 2 orders of magnitude greater than the rate of sea-level rise (Zhang et al. 2004). Thus, sea-level rise may cause a significant loss of sea turtle nesting habitat (Daniels et al. 1993, Fish et al. 2008, Nicholls & Cazenave 2010, Katselidis et al. 2014). This, together with other factors such as the continued increase in storm intensity (Fuentes & Abbs 2010, Knutson et al. 2010), wave energy, height of surge tides (Donnelly 2007, Pye & Blott 2008), and astronomical tidal levels considerably affect coastal changes as well as estimates of total sea level increases (Losada et al. 2013, Reguero et al. 2013).

Some studies have shown that different sea turtle species prefer to nest at about 1 m of elevation about sea level, and will move to another section of the beach or to another beach entirely in order to meet this specific requirement (Hays et al. 1995, Kolbe & Janzen 2002). Many species prefer to emerge on steeper, instead of shallower beaches (Weishampel et al. 2003, Pfaller et al. 2009, Katselidis et al. 2013). In addition, some species preferably nest above the vegetation line in an attempt to avoid storms or the high tide (Horrocks & Scott 1991). Leatherback sea turtles Dermochelys coriacea have a circumglobal distribution, but nesting sites are concentrated at tropical and subtropical latitudes (James et al. 2006). This species exhibits low fidelity to specific nesting beaches/sites, so a leatherback turtle that nests at Pacuare (Costa Rica) could later nest anywhere between Tortuguero (Costa Rica) and Panama (Troëng et al. 2004, Rivas et al. 2016). Leatherbacks tend to nest in the open area between the high tide and the vegetation, although they may occasionally nest below the high tide line (Godfrey & Barreto 1995, Spanier 2010). Because of this proximity to the high tide line when laying their clutches, the species may be more sensitive than others to topographic changes (Whitmore & Dutton 1985, Hays et al. 1995). However, beach parameters such as slopes may determine nest emplacement in other species (Katselidis et al. 2013). Nest site selection affects both hatching success and hatching fitness in sea turtles, and therefore plays a crucial role in maximizing reproductive success (Mrosovsky 1983, Hays et al. 1995). This is why the loss of suitable nesting habitat, as a product of beach erosion, can be an important disruption in terms of nest site selection (Kamel & Mrosovsky 2004), which could potentially reduce the overall reproductive output of leatherback turtles.

The Caribbean serves as a nesting ground to a large population of leatherback turtles (Chacón 1999, Patino-Martinez et al. 2008, Rivas et al. 2016). In this region, the species experiences a natural high loss of clutches due to beach erosion and nest inundation (Santidrián Tomillo & Swiggs 2015). Scarps are generally common in tropical regions, but some beaches such as those in the Caribbean are more dynamic than others (de Alegría-Arzaburu et al. 2013). For instance, Eckert (1987) estimated that environmental unpredictability could result in 45 to 60% annual loss of clutches on some Caribbean beaches. Thus, increased beach erosion due to climate change may become an important threat to the survival of leatherback turtles in the Caribbean, a region where the natural loss of clutches is already high.

In this study, we analyzed the occurrence of dune scarps caused by erosion, as well as their effects on the nesting behavior of leatherback turtles by comparing presence of dune scarps to (1) the number of successful and unsuccessful nesting attempts, (2) nesting success, and (3) nest site selection. Studying how sea turtles respond to beach dynamics at present will allow us to understand the effects that future environmental impacts may have on their populations, especially considering the growing influence of climate change.

MATERIALS AND METHODS

Study site

Our research was conducted at the Pacuare Nature Reserve (PNR), located on the Caribbean coast of Costa Rica. The beach is 5.7 km long and the reserve’s northern and southern limits are at 10°13’ 17” N, 83°16’39” W and 10°10’00” N, 83°14’00” W, respectively. This beach hosts the highest density of leatherback turtle nests in Central America, with a mean density of 142 nests km⁻¹, based on over 18 yr of data (Rivas et al. 2016). The nesting season extends from the beginning of March until the end of July, with the nesting peak occurring in April and May.
PNR’s coastal area is characterized by the presence of dynamic and sandy beaches with slightly steep slopes. The mean tidal range on the Costa Rican Caribbean coast is 0.15 m (Lizano 2006) with a range of 0.40 m at the nearby city of Limón (~40 km from PNR; Instituto Nacional de Meteorología: www.imn.ac.cr). Daily tide levels can sometimes vary by more than 4 m (Menendez & Woodworth 2010), and in spring, the tides can engulf the beach completely, sometimes even reaching the vegetation line (Pugh 1996, Losada et al. 2013).

We placed marker posts from south to north along the beach’s vegetation line to divide it into equidistant 100 m sectors. Post 0 was situated at the southernmost part of the beach and Post 57 at the northern end. We subdivided each of these sectors by placing markers every 25 m. The width of the beach was then divided into 3 zones: the intertidal zone (Zone A); the higher zone of the beach, above the high tide line (Zone B), and the vegetated zone (Zone C).

**Beach morphodynamics**

We observed and monitored the changes in dune scarps throughout the 2013 and 2014 nesting seasons. A scarp was considered as such when its vertical face was higher than 30 cm, and we noted the presence or absence of scarps once a week (every Monday at 16:00 h) in front of each marker post along the beach. We measured the height (h) of each scarp using 2 sticks intersecting at a 90° angle, from the highest point of the crest to the horizontal ground. Additionally, since scarps could be encountered in any of the zones of the beach, we pinpointed their location by measuring the distance from the post to each scarp crest (P-S), and the distance from the bottom of the scarp to the water (S-W) (measured to the previous high tide mark; Fig. 1a). Because scarps could be highly dynamic, we estimated erosion (sand eroded) and accretion (sand deposited) rates and calculated changes in scarp height (cm d⁻¹) every 2 d at 12 of the marker posts, which were chosen depending on where we had observed a previous erosion (posts 13II, 13III, 14, 14I, 14II, 34III, 35, 35I, 35II, 56, 56I, 56II). This estimation was done between 1 April and 31 May 2013.

**Dune scarp effects on nesting behavior and nesting success**

We conducted morning surveys to scan for nesting activities that had occurred during the previous night. In terms of data recording, (1) a nest attempt was considered when a body pit was present, indicating that a turtle had attempted to nest (a ‘body pit’ was considered as an area of sand that had been disrupted) or (2) an aborted attempt was noted when tracks were present without the presence of body pits. We included instances when females were seen
at night and when only the tracks and/or body pits were found at night or in the morning. Nesting success was quantified as the ratio of clutches laid in relation to the total nesting attempts, following Eckert et al. (2012). Additionally, between 2008 and 2014, we calculated the percentage of clutches laid per zone (A, B, or C) in order to identify any changes that may have occurred over time in terms of nest-site selection.

In 2013 and 2014, we determined whether a scarp was present or absent for any nesting activity. If a scarp was present, we measured the height of the scarp (h), the distance from the scarp to the water (S-W), and the distance from the scarp to the nest (S-N) (this distance was measured both when nests were located below or over a scarp; Fig. 1b), after a turtle had nested or aborted. When a scarp was present, we classified nesting behavior into 4 types depending on whether the turtle (1) moved over the scarp and laid eggs (over scarp−laid), (2) moved over the scarp but did not lay eggs (over scarp−aborted), (3) did not move over the scarp and laid eggs below the scarp (below scarp−laid); and (4) did not move over the scarp and aborted the nesting attempt (below scarp−aborted).

We used a long-term data series (1950−2010) comprising monthly mean sea level (MSL) records to determine trends in sea-level rise for the Caribbean coast of Costa Rica. We obtained the data series from the Commonwealth Scientific and Industrial Research Organisation (Church et al. 2004). MSL had been estimated as the average surface level (mm), taking into account the seasonal cycle (monthly mean) and the anomalies in time scales from the monthly variations to the long-term changes (Church et al. 2004, Losada et al. 2013). We smoothed the data with a 10 yr moving average for easier interpretation.

**RESULTS**

**Beach morphodynamics**

In 2013 and 2014, scarps were commonly found and were present at (mean ± SD) 31.0 ± 12.2% and 19.9 ± 8.7% of the 232 beach posts, respectively. These percentages did not differ significantly between years ($\chi^2 = 1.62$, p = 0.203). Scarps were relatively stable, and mean scarp persistence was 50.8 d (Table 1). The mean distance from the vegetation line to the scarp (P-S) varied significantly between marker posts along the beach, showing no trend within (R2 = 0; ANOVA, $F_{6,246} = 16.41$, p < 0.01, 2013; ANOVA, $F_{6,205} = 2.88$, p = 0.01, 2014) and between years (ANOVA, $F_{1,471} = 15.38$, p < 0.001; Table 1, Fig. 2a). The mean change in scarp height, recorded every 2 d, was 6.7 cm d−1 and significantly varied among the 12 selected markers (Kruskal-Wallis test, $H = 24.43$, df = 11, p = 0.01; Table 1, Fig. 2b).

**Dune scarp effects on nesting behavior and nesting success**

The percentage of clutches that were laid between 2008 and 2014 significantly increased in areas which presented a high risk of flooding (Zone A; linear regression, R2 = 0.91, p = 0.001), significantly declined in the open beach area (Zone B; linear regression, R2 = 0.90, p = 0.001), and did not change in the vegetated area (Zone C); linear regression, R2 = 0.26, p = 0.24; Fig. 3).
In 2013, female emergence occurred less frequently in areas that had scarps ($\chi^2 = 33.81, p < 0.001$). In total, 15.7% of nesting attempts (81/515) and 20.9% of nests (n = 68/327) were recorded in areas with scarps. Both the number of nesting attempts and the number of nests km$^{-1}$ were lower in areas with scarps in comparison to those without scarps ($\chi^2 = 8.69, p = 0.003$; Table 2). In contrast, nesting success was greater in areas where scarps were present, although the difference between these areas was not significant ($\chi^2 = 3.53, p = 0.060$; Table 2).

In 2014, females also emerged from the sea less frequently in areas that had scarps ($\chi^2 = 20.0, p < 0.001$). In total, 11.9% (n = 100/837) of nesting attempts and 13.6% (n = 73/537) of nests occurred in areas with scarps. Again, the number of nesting attempts and the number of nests km$^{-1}$ were lower in areas with scarps than without scarps ($\chi^2 = 8.69, p = 0.003$). The difference in nesting success in the presence and absence of scarps was not significant ($\chi^2 = 0.81, p = 0.369$; Table 2).

When looking at the activities in areas with scarps, both the number of nesting attempts and the number of nests km$^{-1}$ were lower in areas with scarps than areas without scarps. However, the difference in nesting success in the presence and absence of scarps was not significant ($\chi^2 = 0.81, p = 0.369$; Table 2).

### Table 2. Percentage and number of leatherback turtle *Dermochelys coriacea* nesting attempts, calculated as the number of nest attempts (considered when clutches were laid or when a body pit was present) plus the number of aborted attempts, in the presence and absence of scarps in 2013 and 2014; number of nesting attempts and nest attempts per km; and percentage of nesting success (ratio of clutches laid in relation to the total nesting attempts; %) in the presence and absence of scarps for the same years

<table>
<thead>
<tr>
<th></th>
<th>Nesting attempts % (N)/per km</th>
<th>Nest attempts % (N)/per km</th>
<th>Aborted attempts % (N)</th>
<th>Nesting success (%)</th>
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<tr>
<td></td>
<td>2013</td>
<td>2014</td>
<td>Total</td>
<td>2013</td>
</tr>
<tr>
<td>Scarps</td>
<td>15.7 (81)/ 45.1</td>
<td>11.9 (100)/ 86.6</td>
<td>20.9 (68)/ 37.8</td>
<td>13.6 (73)/ 63.2</td>
</tr>
<tr>
<td>No scarps</td>
<td>84.3 (434)/ 108.4</td>
<td>88.1 (737)/ 158.6</td>
<td>79.1 (259)/ 64.7</td>
<td>86.4 (464)/ 99.9</td>
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</table>
Nesting success was 55.7% for turtles that remained below scarps and 88.7% for those that moved over them (Table 3). Females aborted nesting attempts more frequently when they were below, rather than over, a scarp ($\chi^2 = 26.11, p < 0.001$). In 2013 and 2014, 6.1 and 3.5%, respectively, of nests laid on the entirety of the beach were located below scarps.

Scarp height influenced nesting behavior. We found significant differences between the mean scarp height next to nests placed above and below the scarp in 2013 (ANOVA, $F_{1,57} = 5.09, p = 0.03$), but these differences were not significant in 2014 (ANOVA, $F_{1,100} = 0.02, p = 0.89$; Table 3, Fig. 4a). Similarly, there were significant differences in scarp height next to areas where females laid or aborted nests in 2013 (ANOVA: $F_{1,81} = 14.55, p = 0.0003$), but not in 2014 (ANOVA: $F_{1,100} = 0.9, p = 0.33$; Fig. 4b). In 2013, females aborted nesting attempts with a greater frequency when the scarp was higher. Considering only the cases when females did not move over the scarp, there were no differences in scarp height between clutches laid and aborted (ANOVA, $F_{1,50} = 1.88, p = 0.18$; Table 3, Fig. 4c).

The mean distance between the scarp and the water (S-W) for females that remained below the scarp and aborted nesting was lower than for those that laid eggs below the scarp (Table 3) (ANOVA, $F = 0.58, p = 0.01$). S-W, including only instances when turtles laid eggs, was significantly different in areas where eggs were laid below vs. over the scarps (ANOVA, $F_{1,98} = 29.7, p < 0.01$; Table 3). In total, 44.8 and 60.3% of nesting females in 2013 and 2014, respectively, laid their clutches in areas with a high risk of flooding (S-W ≤ 5 m). More than 50% of these females laid their clutches within a distance of 2 m below or over the scarp (Fig. 5a).

The presence of scarps did not influence the percentage of nests laid in Zone A compared to those in other zones in 2013 ($\chi^2 = 0.96, p = 0.33$). However, in 2014, significantly more nests were found in Zone A when scarps were present than when they were absent ($\chi^2 = 21.41, p < 0.01$; Table 4).

In terms of the turtles that laid eggs, the distance between the scarp and the nest (S-N) was significantly lower when turtles had not moved over the scarp (0.71 ± 1.35 m) than when they had (4.64 ± 4.25; ANOVA, $F_{1,98} = 34.01, p < 0.01$; Fig. 5b); 80.0% (n = 16) of clutches in 2013 and 89.5% (n = 17) of clutches in 2014 were laid below the scarp within a distance of less than 2 m to the scarp (Table 5).
DUNE SCARP EFFECTS ON NESTING BEHAVIOR AND NESTING SUCCESS

Dune scarps are observed year-round at PNR (M. L. Rivas pers. obs.), but their presence and frequency were never recorded until we began conducting this study. In 2013 and 2014, scarps covered more than 20 to 30% of the whole beach; scarps were recorded by noting their presence every 25 m. A scarp was usually present on average for over 2 mo. Taking into account the fact that the percentage of clutches that are laid in areas with a high risk of flooding has significantly increased over time, we believe that erosion–accretion cycles should be monitored regularly on nesting beaches so that we can characterize both site-specific beach dynamics and changes over time.

**DISCUSSION**

**Fig. 4.** Mean scarp height (m) with respect to leatherback turtle *Dermochelys coriacea* clutches that were (a) laid over or below scarps, (b) laid or aborted (including nests below and over scarps), and (c) laid versus nests aborted below scarps in 2013 and 2014

**Fig. 5.** Scarp distances (m) from (a) the water (S-W) and (b) the nest (S-N) for leatherback turtle *Dermochelys coriacea* clutches laid over versus below scarps at Pacuare Nature Reserve, Costa Rica

**Table 4.** Percentage of leatherback turtle *Dermochelys coriacea* nests (%) laid in Zones A (intertidal zone), B (high beach zone above the high tide line), and C (vegetation) at Pacuare Nature Reserve, Costa Rica
in order to determine the potential effects on sea turtle populations.

Our results show that the presence of dune scarps significantly influenced the nesting behavior of leatherback turtles by (1) reducing the amount of activity in areas where scarps were present, compared to the rest of the beach. It also resulted in (2) a high percentage of females that did not move over scarps and therefore (3) resulted in their clutches being laid below the high tide line. Nests located in these lower areas are more likely to become inundated by tidal action; eggs are more prone to being washed out (Eckert 1987, Caut et al. 2010, Patino-Martinez et al. 2014), and mortality rate is higher due to the decreasing sand temperature (Houghton et al. 2007). Therefore, nest emplacement influences the environment in which clutches develop, potentially decreasing hatchling production (Mrosovsky 1983, Pfaller et al. 2009). Taking into consideration that nest site selection patterns seem to be affected by a variety of environmental factors (Wood & Bjorndal 2000), it seems highly likely that in the future these patterns will be disrupted by these ever-changing processes of erosion.

The effects of climate change may ultimately result in the shifting of nesting sites, as it is possible that turtles will adapt to these increasing levels of erosion by simply moving away to other beaches, if they can find any that are undeveloped and with suitable conditions. In fact, the leatherback sea turtle’s nesting range may already be shifting to higher latitudes (McMahon & Hays 2006). However, if high erosion is present along the Caribbean coast, it will make it more difficult for leatherback turtles to find new places to nest. Consequently, climate change poses new challenges on multiple fronts to which sea turtles will need to respond.

Effects of sea-level rise on nesting habitats

Recent studies have identified sea-level rise and/or increased storm frequency as factors that affect those endangered species whose nesting success depends on the stability of their coastal habitats (Fish et al. 2005, 2008, Fuentes et al. 2010, 2011, Katselidis et al. 2014). Sandy beaches are especially prone to increased levels of erosion (Brown et al. 2013) resulting from storms and tidal level changes (Webster et al. 2005, Pye & Blott 2008).

While global mean sea-level rise is projected to increase, projections might differ substantially among regions (Suzuki & Ishii 2011, Slangen et al. 2012). The sea level on the Caribbean side of Costa Rica increased between 1950 and 2010 (linear regression, $R^2 = 0.83$, $p < 0.001$; Fig. 6). On average, sea level rose 0.2 cm yr$^{-1}$ in that timeframe. If the same trend continues, sea levels could rise by another 20 cm by the end of the 21st century compared to current levels. However, the Intergovernmental Panel on Climate Change’s (IPCC) projections recently predicted a further rise of between 0.40 and 0.63 m for the end of the 21st century, with the most pessimistic scenario predicting these values to range from 0.52 to 0.98 m (IPCC 2013). If these scenarios become a reality in the near future, we may observe dramatic effects on sea turtle nesting grounds.

### Table 5. Percentage of leatherback turtle *Dermochelys coriacea* nests (%) and number of nests (in brackets) classified by their distance to the dune scarps at Pacuare Nature Reserve, Costa Rica. Distances were grouped into 2 m groups

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<tr>
<td>0–2</td>
<td>80 (16)</td>
<td>89.5 (17)</td>
<td>20 (4)</td>
<td>5.3 (1)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5.3 (1)</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>2–4</td>
<td>16.7 (4)</td>
<td>26.5 (13)</td>
<td>54.2 (13)</td>
<td>14.3 (7)</td>
<td>29.2 (7)</td>
<td>20.4 (10)</td>
<td>0</td>
<td>11.3 (6)</td>
<td>0</td>
<td>1.9 (1)</td>
<td>0</td>
<td>20.7 (11)</td>
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**Fig. 6.** Mean monthly sea-level rise (SLR) trend (mm) in the Caribbean region from 1950 to 2010. Data were smoothed with a 10 yr moving average.
Conservation implications

Suitable nesting habitats are decreasing due to anthropogenic and environmental factors (Fish et al. 2008, Mazaris et al. 2009). To mitigate nest loss, sea turtle monitoring projects along this coastline have implemented conservation measures where doomed clutches are relocated to alternative safer locations (Mrosovsky 1983, 2006, Rivas et al. 2016). These clutches are taken to hatcheries or to optimal beach locations. However, this technique could potentially reduce hatching success and alter sex ratios (Spanier 2010, Sieg et al. 2011, Patino-Martinez et al. 2012, Santidrián Tomillo et al. 2012, 2014). Thus, these strategies should be used with caution. Firstly, we suggest conducting an assessment of the quality of the nesting habitat (Mazaris et al. 2009, Torio & Chmura 2013) to develop and prioritize conservation plans (Schlacher et al. 2007). Likewise, long-term studies should be conducted in order to identify whether this species, and other sea turtle species, exhibit phenotypic plasticity in terms of their nesting behavior or whether their risk of extinction is exacerbated due to climate change.

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