NESTING ECOLOGY OF THE PACIFIC GREEN TURTLE IN THE SOUTH PACIFIC OF COSTA RICA

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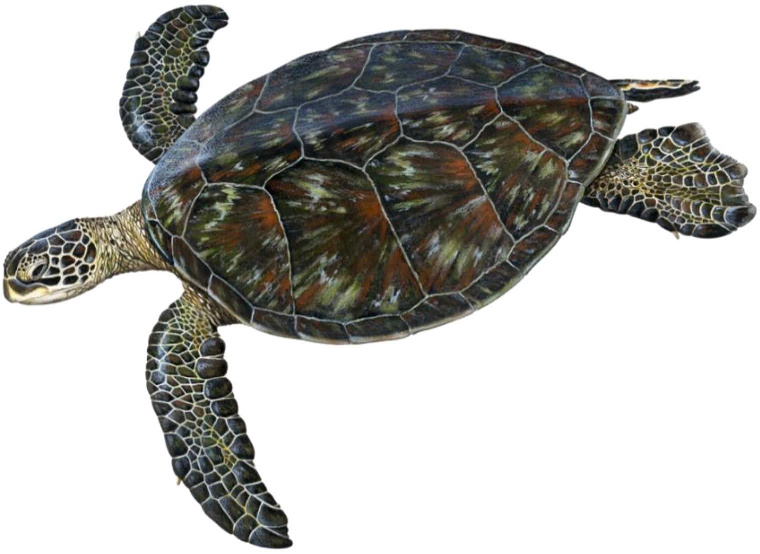

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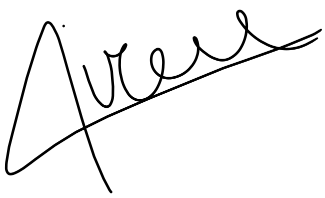

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EXECUTIVE SUMMARY

The Pacific green turtle (*Chelonia Mydas*) nesting population is of conservation importance and has some ecological significance. The current study presents an overview of the nest ecology of Pacific green turtles in the South Pacific of Costa Rica for two nesting seasons (2021–2022 and 2022–2023), focusing on their nesting behaviour, reproductive strategies, and the influence of environmental factors.

The nesting success rates were 20.33% in the season 2021–2022, and 30.65% in the season 2022–2023, with a higher nesting success in the second studied season. The green turtle showed a preference to nest in the upper vegetated part of the beach (zone 3) and in the beach sectors with more vegetation coverage. Hatching and emerging success were significantly higher in nests located in zone 3. Nesting activity had a seasonal trend, with the peak of activity between December and February. The number of nesting attempts per night was significantly higher at nights with the first quarter and last quarter moons in comparison with the full and new moons.

Pacific green turtles in this region exhibited smaller clutch sizes (mean ± SD: 72 ± 20 eggs per clutch) compared with other green turtle nesting populations; however, the observed clutch frequency (OCF) (mean ± SD: 2.574 ± 1.220 clutches in the season 2021-2022 and 2.558 ± 1.104 clutches in the season 2022–2023) and the observed interesting period (OIP) between consecutive oviposition events (mean ± SD: 12.643 ± 2.341 days and 12.267 ± 2.314 days in the seasons 2021–2022 and 2022–2023, respectively) fell within the range reported for green turtles. Clutch size increased with female size.

Conservation efforts for the Pacific green turtle in Costa Rica should take into important consideration the ecological, biological, and behavioural characteristics of a nesting population as well as their adaptation capacities to climate change effects. Moreover, education and outreach programs to raise awareness about the importance of preserving nesting habitats should be taken into account in a proper conservation plan. Continued research and long-term monitoring of nest ecology are essential for developing effective conservation strategies and ensuring the management and recovery of this population.

ABSTRACT

Green turtle (*Chelonia Mydas*) populations suffer different types of threats that compromise their survival and reproduction. For their ecological roles and as umbrella species, they are of conservation importance.

Since green turtles are terrestrial nesters, nesting beaches provide an important opportunity for studying their nesting biology and behaviour, which are related to their reproductive fitness and thus to their conservation.

This study has as a main goal to conduct an exhaustive analysis of the nesting ecology and behaviour of Pacific green turtles on two beaches in the South Pacific of Costa Rica during two full nesting seasons.

Results show the main trends in nesting activity on two nesting beaches, the spatial and temporal distribution of the nesting activity, the influence of some environmental factors on the nesting and reproductive processes, and strategies that nesting turtles adopt in order to increase the chances of successful reproduction and enhance the survival of the green turtle population.

An understanding of the nesting environment, ecology, and behaviour of a population is crucial for its conservation and management in the region.

1. INTRODUCTION

The green turtle (*Chelonia Mydas*) is one of the seven living species of sea turtles in the world. As unique components of complex ecosystems, sea turtles have important roles in coastal and marine habitats by contributing to the health and maintenance of coral reefs, seagrass meadows, estuaries, and sandy beaches (Eckert et al., 1999). Furthermore, marine turtles can be considered an umbrella species, which means that conserving them and their habitats can help to protect multiple other species and thus sustain marine biodiversity (Dickson et al., 2022).

The marine turtle populations suffer nowadays different types of threats, including, on the one hand, direct anthropogenic-induced stressors such as hunting and egg consumption and, on the other hand, indirect human-induced stressors including fisheries impacts, urban development, and pollution (Poloczanska et al., 2009). An additional factor that compromises marine turtle reproduction is nest depredation by wild animals and domestic dogs (Exley et al., 2022). Moreover, climate change, global warming, and alterations in their breeding habitats are some of the main hazards to marine turtles (Hamann et al., 2021; Poloczanska et al., 2009). All sea turtle species are included on the IUCN Red List of Threatened Animals (Eckert et al., 1999). Green turtles, in particular, are globally classified as endangered (Bell et al., 2007).

Green turtles are mainly found in tropical and subtropical waters (Seminoff, 2004). They are highly migratory, long-lived species with delayed sexual maturity and high adult survival but low hatchling survival (Bourjea et al., 2007).

As the other seven species of sea turtles, green turtles are marine-adapted reptiles, and therefore, they spend most of their life cycle in the marine environment (Mutalib et al., 2014; Nishizawa et al., 2013; Okuyama et al., 2012). Despite this, they are obligate terrestrial nesters, and they are also ecologically significant in the terrestrial ecosystem (Nishizawa et al., 2013).

The nesting process normally occurs at night as a reflection of adaptation to heat stress and diurnal predators (Bowen et al., 1992). This nesting process involves a sequence of behavioural phases: emerging from the ocean, crawling up the beach to find a suitable nesting site, clearing the nest site by doing a body pit, digging an egg chamber, depositing the eggs within the chamber, covering it, camouflaging the nest site to hide it from predators, and returning to the sea (Ekanayake et al., 2011; Nishizawa et al., 2013). Turtles do not lay eggs during every nesting activity (Ekanayake et al., 2011). For a variety of reasons, they may abandon the nesting efforts at one of the stages of the nesting process and return to the sea without depositing a clutch, which is called a false crawl (Bjorndal et al., 1999; Ekanayake et al., 2011).

Eggs, once deposited, are abandoned by the female adult, and they are incubated in the warm and moist confines of the nesting chamber (Ackerman, 1980). The egg incubation period for the green turtle ranges from 55 to 70 days (Prieto & Harrison, 2012; Santidrian et al., 2015; Zárate et al., 2013). Finally, the successful hatchlings dig their way up to the beach surface and disperse into the ocean (Ackerman, 1980).

Sea turtles, like other reptiles, do not provide parental care. This is why they have a distinct sensibility to the physical and climatic conditions throughout egg incubation and embryonic development. In addition, environmental conditions play a fundamental role in the hatchling sex ratio and the success of hatchlings (Zavaleta-Lizárraga & Morales-Mávil, 2013).

Green turtles lay several clutches per nesting season (Davenport, 1997). Between nesting events, females rest in nearshore waters to prepare their eggs for the next clutch. On the other hand, they do not breed every year (Shimada et al., 2021). Green turtles show nest site fidelity to specific breeding areas, and every few years, adult females return to the same natal nesting areas to lay (Shimada et al., 2014; Shimada et al., 2021). This makes them even more vulnerable to climate change, alterations in their nesting habitats, and anthropogenic threats (Shimada et al., 2021).

Important green turtle nesting rookeries are found on mainland shores in Costa Rica (Ekanayake et al., 2011). The Eastern Pacific subspecies of the green sea turtle (*Chelonia mydas agassizii*), known locally as the Pacific black turtle, is one of the nesting populations present on the Pacific side of Costa Rica (Hunt & Vargas, 2018). Although there is extensive scientific information on the population biology and nesting ecology and behaviour of green turtles, very few detailed studies have been focused on the Eastern Pacific populations (Santidrian et al., 2015).

The sea turtle nesting beaches provide a narrow but important window of opportunity for studying their reproduction and nest biology, which are also related to their reproductive fitness (Eckert et al., 1999). An understanding of the reproduction and nesting ecology and behaviour of sea turtles, the impacts of human activities on the nesting process, the characteristics of the beaches where they nest, and their reproductive success is essential for the management and recovery of sea turtle stocks in the region and for their conservation (Eckert et al., 1999; Nishizawa et al., 2013).

The aim of this study is to conduct an exhaustive analysis and a beach characterization regarding the nesting ecology and behaviour of the Eastern Pacific green turtles on two nesting beaches in the South Pacific of Costa Rica, during the full nesting seasons 2021–2022 and 2022–2023.

2. MATERIAL AND METHODS

2.1. AREA OF STUDY

The study area is located on the Osa Peninsula, in the southwest corner of Costa Rica, which is considered one of the most biodiverse spots of the country if not of the world (Sellés-Ríos et al., 2022; Friedlander et al., 2022).

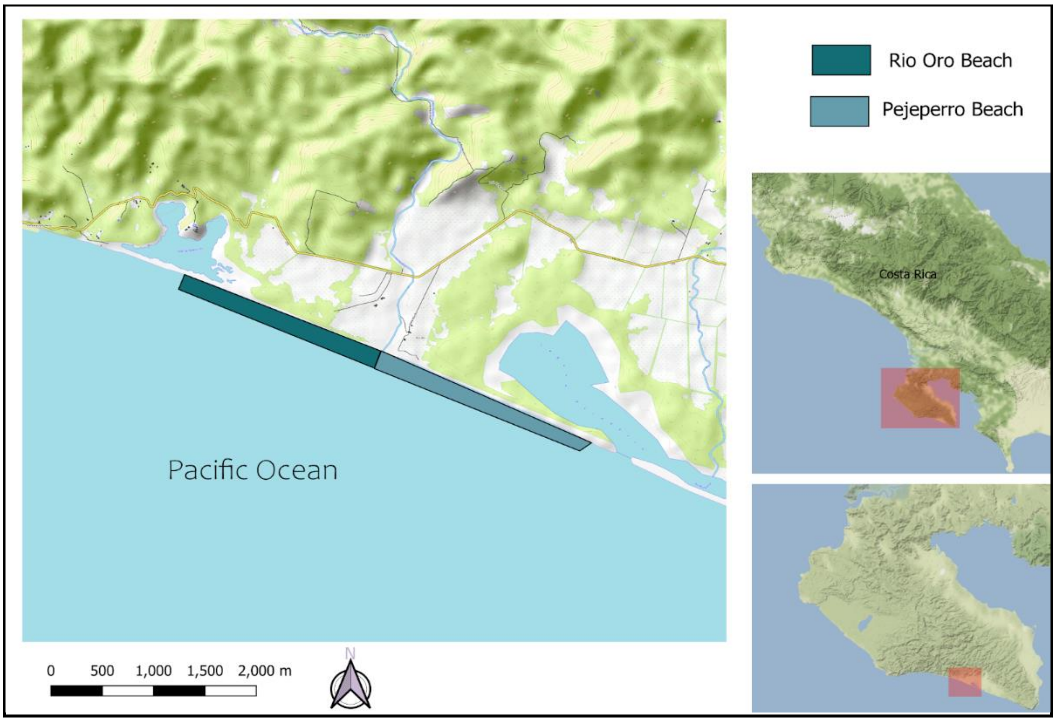

Figure 15. Map of the study area. Source: self-made map with q-GIS.

The monitoring was carried out along two sea turtle nesting beaches on the southern part of the peninsula, in the south Pacific Coast: Pejeperro beach (8°26'12.46″N, 83°23'59.90″W) and Rio Oro beach (8°32'08.95″N, 83°18'14.09″W).

Rio Oro beach is 3 km long, extending from Pejeperrito coastal lagoon to the mouth of the Rio Oro River. On the other hand, Pejeperro beach is 3,5 km long from the mouth of the Rio Oro River to the Pejeperro coastal Lagoon (Figure 1) (Ávila-Aguilar, 2015; C. R. I., 2013). Both beaches are highly inclined and washed over by tides, and the sand composition differs along the beaches between fine and pebbly (Sellés-Ríos et al., 2022).

Figure 16. Pejeperrito coastal lagoon and Rio Oro beach. Image made by the intern Lars Bendels using a drone.

The coastal lagoons, which define the limits (Figure 2) of the beaches, are vulnerable and important ecosystems with mangrove swamps and flooded forests, and they are breeding sites for many amphibians, reptiles, and birds (C. R. I., 2013). In addition, the strong connection between freshwater and marine environments in these regions highlights the importance of healthy land-sea connections for ecosystem productivity in the area (Friedlander et al., 2022). The surrounding terrestrial habitats consist mainly of lowland rainforest, highland cloud forest, jolillo palm forest, and mangrove swamps (Friedlander et al., 2022).

The study area belongs to the Pejeperro and Rio Oro Wildlife Refuges, which are managed under the Área Conservación Osa (ACOSA) (Quesada-Alpíza & Cortes, 2006). They are remarkably rich in terrestrial and marine biodiverse habitats and species, and they have relatively low coastal development (Quesada-Alpíza & Cortes, 2006; C. R. I., 2013). However, the biodiversity and marine-coastal environments have been degraded by human activities, mainly because of the rapid expansion of agricultural, tourism development and land contamination (Arozarena et al., 2015; Friedlander et al., 2022).

The weather in this part of the south Pacific in Costa Rica is hot and humid. It is characterized by a pronounced rainy season with heavy rainfalls that are especially intense from August to early December and a dry season from late December to April in which the rain diminishes, the temperatures are higher, and there are more hours of sun (Quesada-Alpíza & Cortes, 2006; Brumberg et al., 2021). Mean annual temperatures range from 24.5 °C to 26.5 °C, and rainfall ranges from 3000 to 7000 mm (Brumberg et al., 2021). Due to the high rainfall and steep terrain in this region, there are strong land-sea linkages that can have positive effects on the marine environment, such as nutrient enrichment, but also negative effects, like sedimentation (Friedlander et al., 2022).

The area is lightly populated and is one of the most socioeconomically disadvantaged regions of Costa Rica (Friedlander et al., 2022). Appropriate small-scale development may be balanced with some environmental practices to provide sustainable social and economic opportunities (Friedlander et al., 2022).

2.2. BEACH MONITORING

Both beaches were divided into sectors every 25 m, from west to east, in the parallel axis to the tide line using marks in the vegetation (i.e., 88, 88.25, 88.5, 88.75). In order to simplify the data interpretation and analysis, these sub-sectors were grouped four by four with sectors of 100 meters. In addition, three different zones were distinguished in the perpendicular line from the water to the vegetation: zone 1; below the high tide line; zone 2; between the high tide line and the vegetation line (intertidal zone); and zone 3; in the vegetation.

The beaches were patrolled at night for a minimum of 4 hours. Considering that turtle emergence can be related to the tides (Reina et al., 2002), having more nesting activity with higher tides and during the rise of the tide (Reina et al., 2002), preferably the patrols started at times when there was high tide or when the tide was rising. The objective of these night patrols was to identify or tag and take biometric data from all the female turtles found, as well as mark and record data from the nesting events.

During the morning census, all the tracks indicating all the nesting events that occurred the night before were recorded. It was registered as a confirmed nest (N) when the turtle performed all the nesting steps, including egg laying, with success and as a false crawl (RF) when the turtle went back to the sea without laying the eggs. The percentage of nesting success was calculated as the proportion of the confirmed nest from the total nesting attempts. When there was evidence that the eggs were taken by humans, it was recorded as poaching (S) and as predation (P) when the eggs were eaten by an animal. In addition, during the mornings, the previously marked nests that were nearby the hatch were checked. For each track/nest event, the sector, and the zone in which they were founded were also recorded. Moreover, the moon phase and the highest tide that occurred during the previous night were registered.

The beaches were monitored through morning census and night patrols during the seasons 2021-2022 and 2022-2023, from the beginning of June until the end of February in the first studied season and from June to March in the second season. Taking into account that the main biologic camp is situated next to the mouth of the Rio Oro River, for some days during the rainy season, the surveys weren't carried out since the beaches were inaccessible as a consequence of the increase in river flow.

2.3. DATA COLLECTION

2.3.1. NESTING TURLTES

The data collection started with recording the turtle species, the local time, and the activity that the turtle was doing at the moment it was found. Subsequently, the following nesting activities and the local time in which they were carried out were also recorded. During the hole nesting process, seven different activities were registered: going up: if the turtle was ascending from the water to the nesting zone, digging a body pit: when the turtle found the proper place to lay the eggs and started clearing out the sand in order to avoid a nest collapse, digging an egg chamber, laying eggs: in the moment the turtles started laying the eggs, covering the nest: at the moment she covered the egg chamber with sand, camouflaging the nest: when she put sand and other materials on the nest and the surroundings with the purpose of hiding it, and finally returning to the water: when the turtle started going back to the sea. The sector and the zone in which the nesting process was realized were also noted. For the turtles that returned to the sea without laying eggs, the same data was collected, but it was registered as a false crawl.

Once the turtle started spawning, the number of eggs laid was counted to register the clutch size, and a metal plate with the turtle spices, the date, the hour in which the turtle was seen for the first time, and the people who were collecting the data were introduced into the nest chamber.

The tagging and turtle measurements were performed once the egg-laying was complete. First, the turtle was checked in order to verify if she was already tagged with an external INCONEL metal tag, and she was marked if she had none. Due to the possibility of tag loss, the turtle was double-tagged, with one tag on each of the two front flippers (Figure 3). The tagging site used was the second scales of the front flippers. The identification code present on the INCONEL metal tag was noted down inside a square if the turtle was already marked (to indicate that the turtle was a recapture) and without the square if the tag was new.

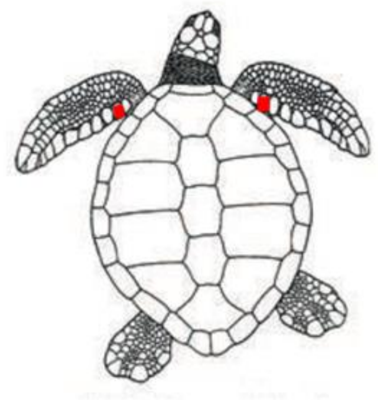

Figure 17. Nesting turtle tagging sites. Picture edited from Martínez et al., 2011.

After the turtle was identified or tagged, her curve carapace length (CCL) and width (CCW) were measured with a flexible measuring tape. The CCL was measured from the anterior point at midline (nuchal scute) to the posterior notch at midline between the supracaudals (Figure 4). For the CCW, the length running across the carapace from one lateral scale to the other at the widest point was measured (Figure 4) (De Boer et al., 2021). Both measurements were taken three times each.

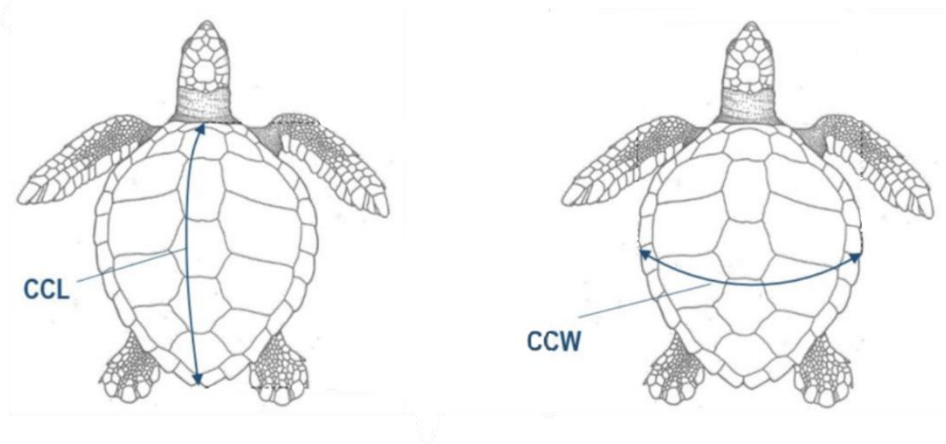

Figure 18. Curve carapace length (CCL) and width (CCW). Picture edited from De Boer et al., 2021.

Finally, the nesting turtle was checked to see whether she had any injuries, scars, or epibionts, as well as signs of illness or unfavourable health conditions.

The observed interesting periods (OIP), which are the number of days between confirmed nesting events, were calculated for each turtle (Santidrian et al., 2015). The OIP values that were twice as long or longer than the minimum OIP were eliminated because the turtle could have been missed in between observed nesting events (Santidrian et al., 2015). The number of confirmed nests for each turtle was also determined and defined as the observed clutch frequency (OCF) (Santidrian et al., 2015).

2.3.2. NESTS

The nests were marked during the night patrols while the turtles were laying the eggs by triangulation to know the exact location of the nest. To do so, the distance from the nest chamber to the closest sector markers to the west and east was measured. A third point was placed in the vegetation, in a straight line from the nest. This additional point was marked with a flagging tape that had information about the turtle species and the date of the oviposition. The distance between the nest chamber and the knot of the flagging tape was also measured, having like this a total of three distances. Moreover, the north and west GPS coordinates were registered within three meters of precision. In case there was a risk that some nests were going to be poached or flooded by the tide, they were relocated to a safer place on the beach with similar conditions to the original one. Ideally, the eggs relocation was done right after the turtle finished laying them or as soon as it was possible and secure. In this eventuality, the triangulation distances and the GPS coordinates were taken only when the nest had already been relocated. During the morning census, all the triangulations executed the night before were verified, and they were redone in case there was any possible mistake in one or more of the distances.

In addition, throughout the morning census, those nests that were close to their hatching were monitored. The incubation period for green turtle (*Chelonia Mydas*) nests ranges from 55 to 70 days (Prieto & Harrison, 2012; Santidrian et al., 2015; Zárate et al., 2013). Therefore, from the day 55th, it was checked every day if there were any clues that indicated that the neonate turtles had already hatched the eggs or/and emerged from the nest. A slight depression indicated that the neonates had started the egg hatching, as the sand collapsed into the space vacated by the hatchlings. The hatchlings' tracks observed from the nest to the water were a sign that the neonates were already emerging from the nest (Stapleton & Eckert, 2008).

The nests were exhumed with the purpose of determining the hatching success, the emerging success, and the fertility. They were exhumed 72 hours after observing the first baby tracks, which indicated the emergence of the first hatchlings (Calderón & Ricardo, 2021), or 10 days after the estimated date of hatching if any signs of birth were recorded.

For every exhumed nest, the number of alive and dead neonate turtles, hatched eggs, pippeds, unhatched eggs, and indeterminate eggs was registered. The presence of fungus, bacteria, larvae, and insects on the eggs or in the nest, as well as other observations such as malformations in the neonates, were also recorded.
They were considered hatched eggs, those eggshells that presented more than 50% of the shell in a single piece.
They were considered pippeds, those eggs that the new-born turtles had begun to open but had not completely left the shell. There were either live pippeds, in which alive newborns were helped to peel off the remains of their shell, or dead pippeds, in which neonate turtles were dead.

The unhatched eggs were opened, and they were classified into 5 embryonic development stages according to the space that the embryo occupied within the egg, following the methodology of Chacón & Sánchez (2023).

Stage 0: The egg is not fertile, and there is no embryo inside.
Stage I: The embryo covers 0 to 25% of the amniotic cavity of the egg.
Stage II: The embryo covers 26 to 50% of the amniotic cavity of the egg.
Stage III: The embryo covers 51 to 75% of the amniotic cavity of the egg.
Stage IV: The embryo covers 76 to 100% of the amniotic cavity of the egg.

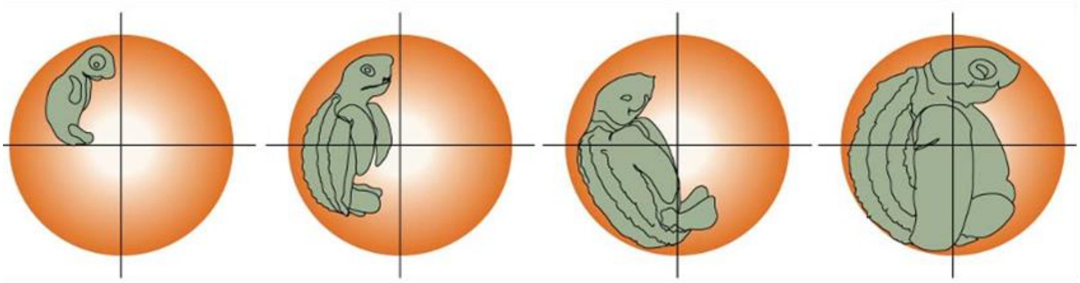

Figure 19. Embryonic development stages. Picture extracted form Chacón & Sánchez (2023).

Unhatched eggs were registered as unknown if it was impossible to assess at which embryonic stage the development was stopped.

Finally, the eggs were recorded as indeterminate when they had hatched, but the neonate turtles were in decomposition, so they couldn't accurately be classified into any of the above categories.

The hatching and the emerging success (%) were estimated using the following formulas:

$$\text{Hatching success} = \frac{\text{Hatched eggs}}{\text{Total number of eggs}} \; x \; 100$$

$$\text{Emerging success} = \frac{(\text{Hatched eggs} - \text{Alive neonates} - \text{Dead neonates})}{(\text{Total number of eggs})} \; x \; 100$$

The fertility (%) of the clutch was estimated using the following formula:

$$\text{Fertility} = \frac{(\text{Hatched eggs} + \text{Unhatched eggs in development} + \text{Pippeds} + \text{Indeterminate})}{(\text{Total number of eggs})} \; x \; 100$$

Where the unhatched eggs in development are those unhatched eggs that were classified in embryonic development stages I, II, III, and IV.

In all formulas, the total number of eggs includes the sum of hatched eggs, pippeds, total unhatched eggs (with and without apparent development), and indeterminate eggs.

2.4. DATA ANALYSIS

The data visualization and all statistical analyses were performed using Rstudio software.

Shapiro-Wilk was used to test the normality of continuous data. All continuous data presented normality ($p > 0.05$) except for hatching, emerging success, and fertility ($p < 0.05$).

The chi-square test was used to study if there were differences in nesting activity in the two studied seasons and beaches, as well as nesting site preferences.

An analysis of variance (ANOVA) was used to assess the effect of the moon phases on the total nesting events per night. It was also employed for comparison of the hatching and emerging success among the two studied beaches and beach zones and to study the effect of the monthly nesting on the clutch size and fertility.

Post hoc tests were performed after finding a significant result in an overall analysis of variance (ANOVA) to determine specific pairwise comparisons between groups.
Linear regressions were carried out in order to study the relationship between female body sizes and clutch sizes.

A significance level of $p < 0.01$ was employed for the chi-square test, the analysis of variance (ANOVA) test, the linear regressions and the post hoc test.

3. RESULTS

3.1. NESTING ACTIVITY

A total of 257 confirmed nests were registered during the season 2021–2022: 118 in Pejeperro Beach (PP) and 139 in Rio Oro Beach (RO) (Figure 6); and 1007 false crawls, 540 in Pejeperro (PP) and 467 in Rio Oro (RO) respectively (Figure 6), were recorded during this season. The nesting success rate in Pejeperro Beach was 17.93% and 22.94% in Rio Oro Beach. The total nesting success of this season was 20.33%.

Regarding the season 2022–2023, the total number of confirmed nests was 346: 149 in Pejeperro (PP) and 197 in Rio Oro (RO) (Figure X). And the false crawls noted were 783: 366 in Pejeperro (PP) and 417 in Rio Oro (RO) (Figure 6). The nesting success rates on Pejeperro and Rio Oro beaches were 28.93% and 32.08%, respectively. The total nesting success of this season was 30.65%.

No significant differences in the total nesting activity (considering the confirmed nests and the false crawls) were detected between Rio Oro and Pejeperro beaches in any of the two seasons studied [χ^2 (df = 2, n = 1264) = 4.877, P = 0.087 for the season 2021-2022; χ^2 (df = 2, n = 1129) = 1.301, P = 0.520 for the season 2022-2023]. Neither did the turtles have a preference for nesting on one of the two beaches during these seasons [χ^2 (df = 1, n = 257) = 6.659, P = 0.190 for the season 2021-2022; χ^2 (df = 1, n = 346) = 1.301, P = 0.0199 for the season 2022-2023].

Since there weren't significant differences regarding the total nesting activity between the two studied beaches for the rest of the study, these beaches were analysed together.

Although in both studied seasons the nesting turtles tend to make significantly more false crawls than successful nests [χ^2 (df = 1, n = 2393) = 32.755, P <0.001], the confirmed nets were significantly higher during the season 2022-2023 than the previous season [χ^2 (df = 1, n =603) = 13.136, P <0.001].

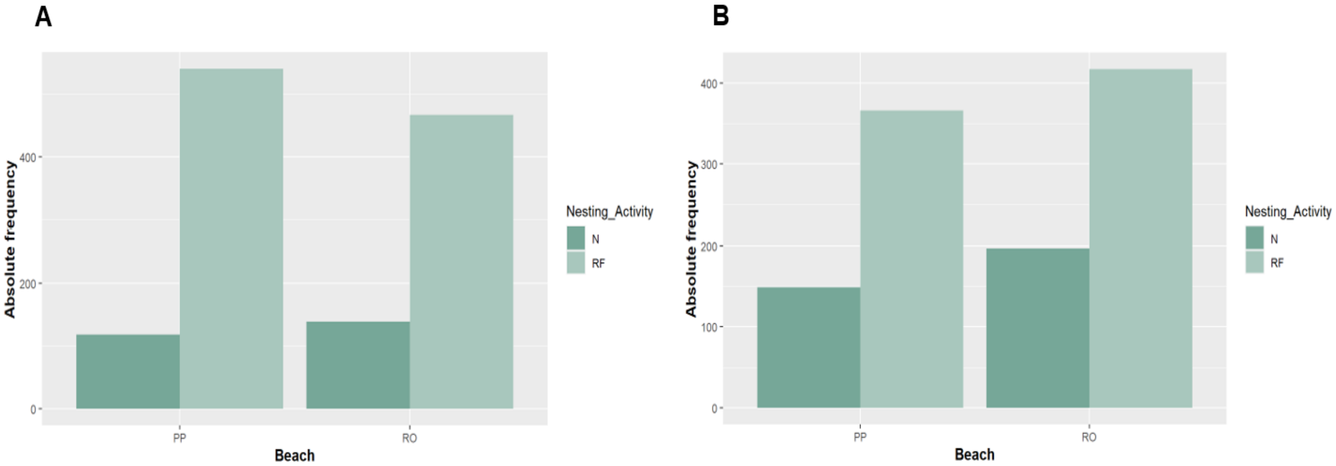

Figure 20. Total number of confirmed nests and false crawls recorded during seasons 2021-2022 (A) and 2022-2023 (B).

3.2. TEMPORAL DISTRIBUTION

The nesting activity at Pejeperro and Rio Oro beaches had a seasonal trend. The months with more nesting activity were from October to February for the season 2021-2022, and from October to March for the season 2022-2023. The peak of nesting activity for both seasons was between December and February.

The month with the highest number of nests was January, with 55 confirmed nests in the season 2021-2022 (Figure 7) and 86 in the season 2022-2023 (Figure 7).

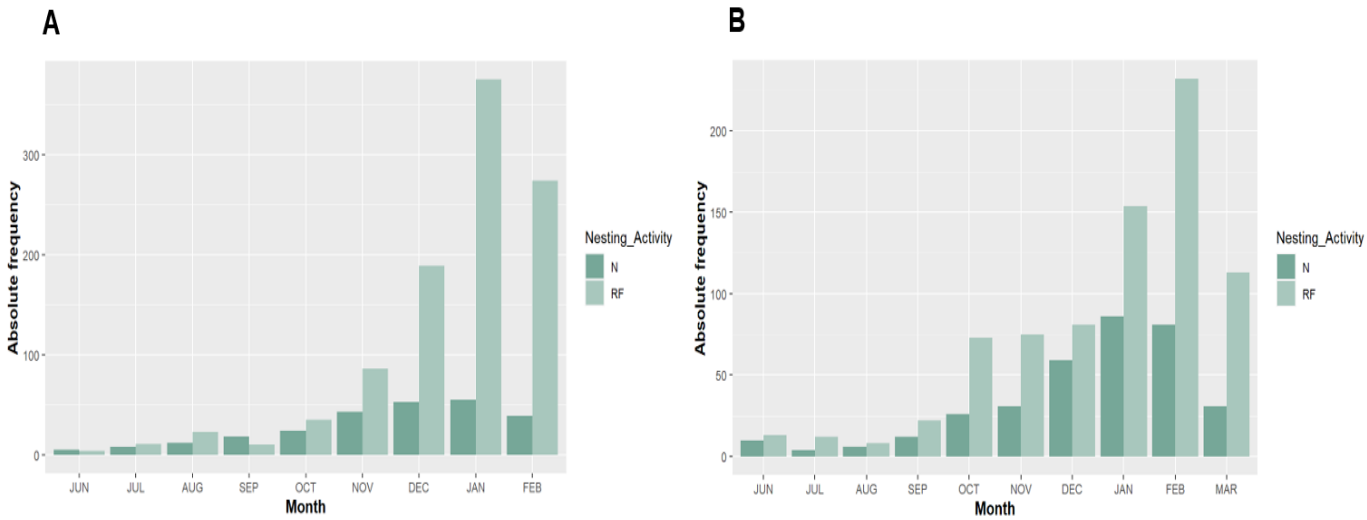

Figure 21. Total number of confirmed nests and false crawls per month during seasons 2021-2022 (A) and 2022-2023 (B).

3.3. SPATIAL DISTRIBUTION

3.3.1. VERTICAL DISTRIBUTION

A total of 8, 86, and 163 were placed in zones 1, 2, and 3, respectively, during the season 2021-2022 (Figure 8); and 5, 92, and 249 during the season 2022-2023 (Figure 8). For both seasons, green turtles showed a preference to nest in zone 3 [χ^2 (df = 2, n = 257) = 140.23, P <0.001 for the season 2021-2022; χ^2 (df = 2, n = 346) = 265.18, P<0.001 for the season 2022-2023].

Concerning the false crawls, 56, 397, and 330 were given in zones 1, 2, and 3, respectively, during the season 2021-2022 (Figure 8); and 182, 418, and 407 during the season 2022-2023 (Figure 8). The nesting attempts without success were also dependent on the zone, with higher false crawls in zone 3 but especially in zone 2 [χ^2 (df = 2, n = 1007) = 105.7, P= <0.001 for the season 2021-2022; χ^2 (df = 2, n = 765) = 250,12, P<0.001 for the season 2022-2023].

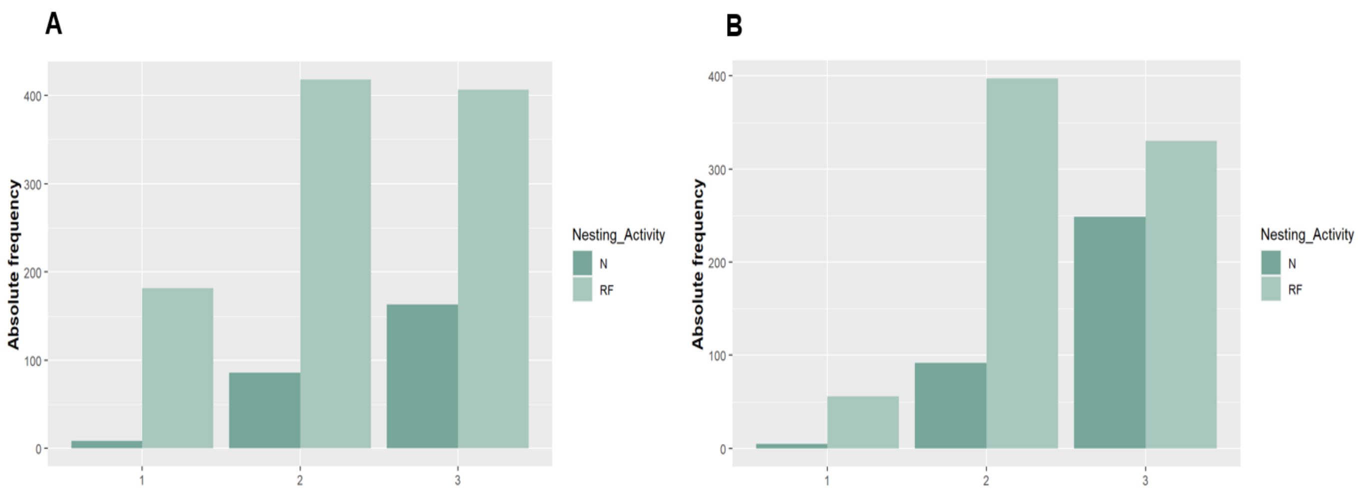

Figure 22. Total number of confirmed nests and false crawls per beach zone during seasons 2021-2022 (A) and 2022-2023 (B).

3.3.2. HORITZONAL DISTRIBUTION

The horizontal distribution was just studied for the season 2022-2023, since no data was available for the previous season.

Regarding the horizontal on Pejeperro Beach, green turtles (Chelonia Mydas) nested along the entire beach apart from the sector situated next to the Rio Oro's River mouth (RIO) and the last sector located next to the Pejeperro coastal lagoon (FINAL) (Figure 9). Sector 81 showed a higher nest occupancy when compared to other sectors. From sectors 80 to 84 and from sectors 86 to 89, these were the areas most chosen by green turtles (Chelonia Mydas) to nest. Sector 85 is the sector that presented fewer nests and more false crawls (Figure 9).

On the Rio Oro beach, the area with the highest nesting activity and the largest number of confirmed nests was concentrated from sector 63 to sector 73 (Figure 9). Sector 67 was the one with the most nests on the entire beach. The sectors that were situated close to the Pejeperrito Coastal Lagoon and the Rio Oro's River mouth were the ones with the fewest confirmed nests.

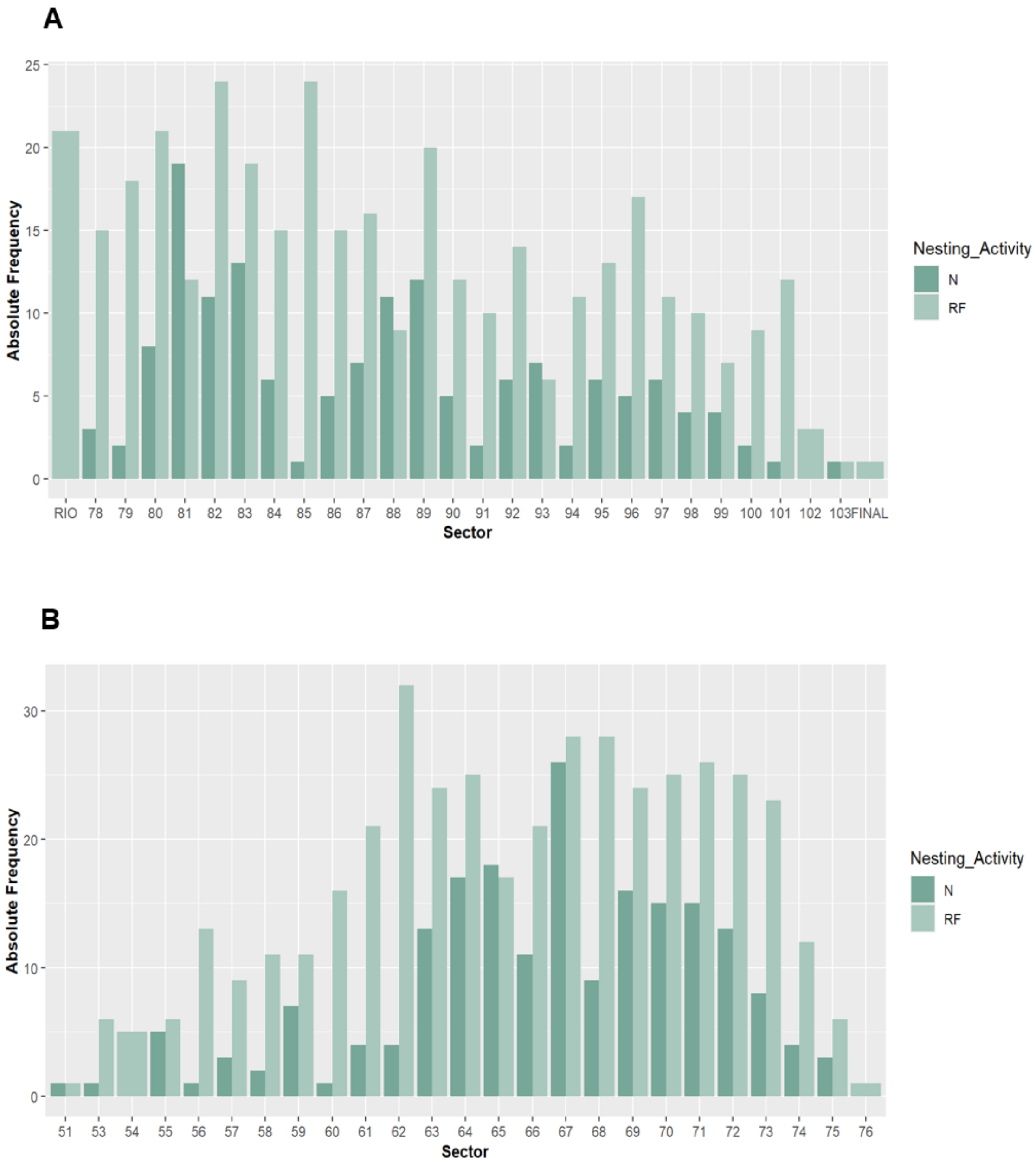

Figure 23. Total number of confirmed nests and false crawls per beach sector in Pejeperro Beach (A) and Rio Oro Beach (B) during the season 2022-2023.

3.4. EFFECT OF THE MOON PHASES ON THE NESTING ACTIVITY

Figure 10 shows all the nesting activities—confirmed nests as well as false crawls—recorded on the two monitored beaches at specific moon phases during the two full study seasons. A total of four moon phases were considered: the first quarter, full moon, last quarter, and new moon.

For both seasons, the total nesting events were dependent on the moon phase [χ^2 (df = 3, n = 140) = 23.486, P <0.001 for the season 2021-2022; χ^2 (df = 3, n = 173) = 42.468, P<0.001 for the season 2022-2023].

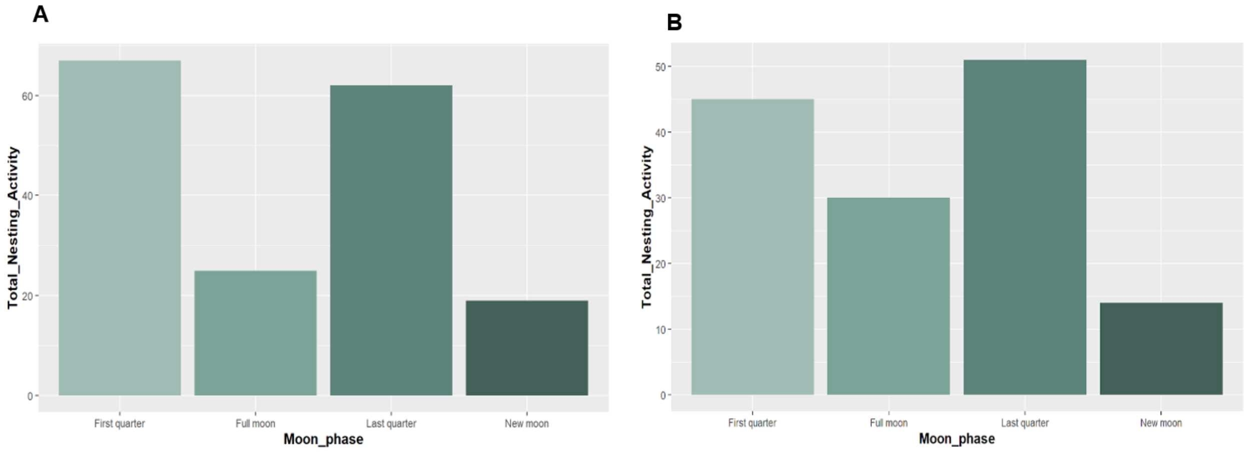

Figure 24. Total nesting events recorded during the full seasons 2021-2022 (A) and 2022-2023 (A) when the moon phase was first quarter, full moon, last quarter, or new moon.

Moreover, Figure 11 shows the distribution of the nesting events that were recorded on a night with the first quarter moon, full moon, last quarter moon, and new moon during the months with more nesting activity (November, December, January, and February) of the two studied seasons.

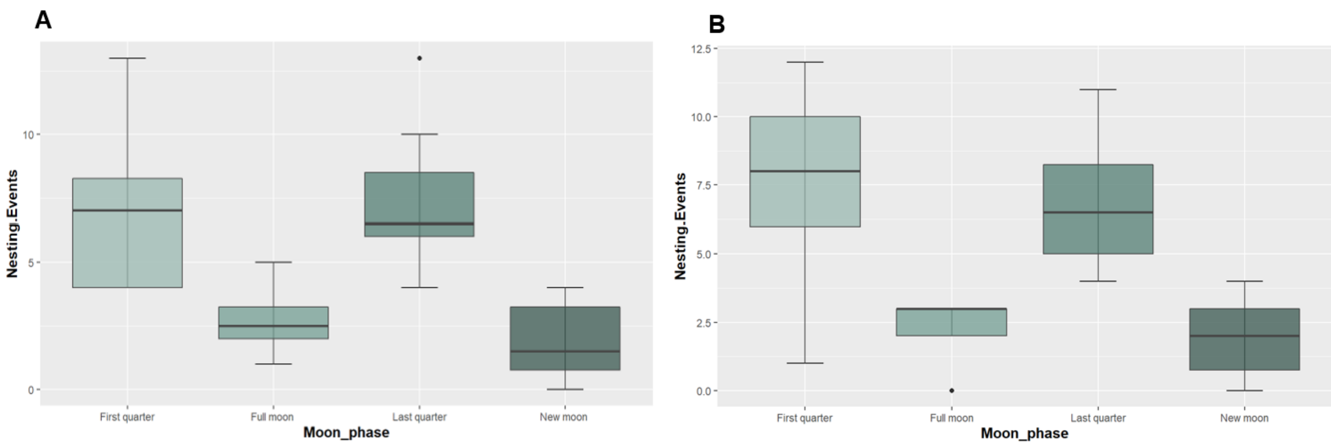

Figure 25. Distribution of the number of nesting events per night that occurred at nights with moon phases: first quarter, full moon, last quarter and new moon in the months with more nesting activity in the seasons 2021-2022 (A) and 2022-2023 (B).

Both in seasons 2021–2022, and 2022–2023, the moon phase had an overall effect on the number of times that the nesting turtle emerged in a night (ANOVA test, F value = 4.259, P<0,01; ANOVA test, F value = 11,883, P<0.001 respectively).

For both studied seasons, the mean of the turtle emergences per night with the first quarter moon and the last quarter moon were significantly different from nights with the new moon and full moon (pairwise t-test, p values < 0.01).

The means of the number of total nesting events registered at nights with the first quarter moon and the last quarter moon (7.000 ± 3.162 and 7.500 ± 2.828 respectively for the season 2021-2022; and 5.500 ± 4.506 and 6.167 ± 1.941 for the season 2022-2023) were significantly higher than the means of total nesting events at nights with the full and new moon (2.750 ± 1.282 and 1.875 ± 1.642 respectively for the season 2021-2022; and 2.833 ± 1.602 and 1.167 ± 1.472 for the season 2022-2023).

3.5. NESTING FEMALES

3.5.1. BIOMETRICS AND REPRODUCTIVE OUTPUT

A total of 179 green turtles (Chelonia Mydas) were measured in Pejeperro and Rio Oro beaches during the two studied seasons: 107 during the season 2021-2022 and 72 during the season 2022-2023. The CCL was (mean ± SD) 86.426 ± 7.307 cm and the CCW was 81.369 ± 5.844 (n = 179) (Table 1).

Table 1. CCL and CCW (mean ± SD) of the nesting female green turtles (Chelonia Mydas) during the full study seasons.

	N	***CCL***	***CCW***
SEASON 2021-2022	107	86.003 ± 7.657	81.080 ± 5.932
SEASON 2022-2023	72	87.015 ± 6.758	81.793 ± 5.728
TOTAL	179	86.426 ± 7.307	81.369 ± 5.844

The clutch size (mean ± SD) was 69 ± 23 for the season 2021-2022 and 75 ± 16 for the season 2022-2023 (Table 2). There were no significant differences in clutch size between the seasons 2021-2022 and 2022-2023 (n = 121, F value = 2.393, P = 0.125). The clutch size for the total studied period was 72 ± 20 (Table 2).

Table 2. Clutching size of the nesting female green turtles (Chelonia Mydas) during the full study seasons.

	N	*CLUTCH SIZE*
SEASON 2021-2022	62	69 ± 23
SEASON 2022-2023	58	75 ± 16
TOTAL	121	72 ± 20

3.5.2. CLUTCH SIZE OVER TIME

Neither in season 2021-2022, nor in season 2022-2023, there were significant differences in the number of eggs released by a female turtle (clutch size) as months went by throughout the season (n = 55, F value = 0.693, P=0.561; n = 66, F value = 0.162, P=0.957 respectively).

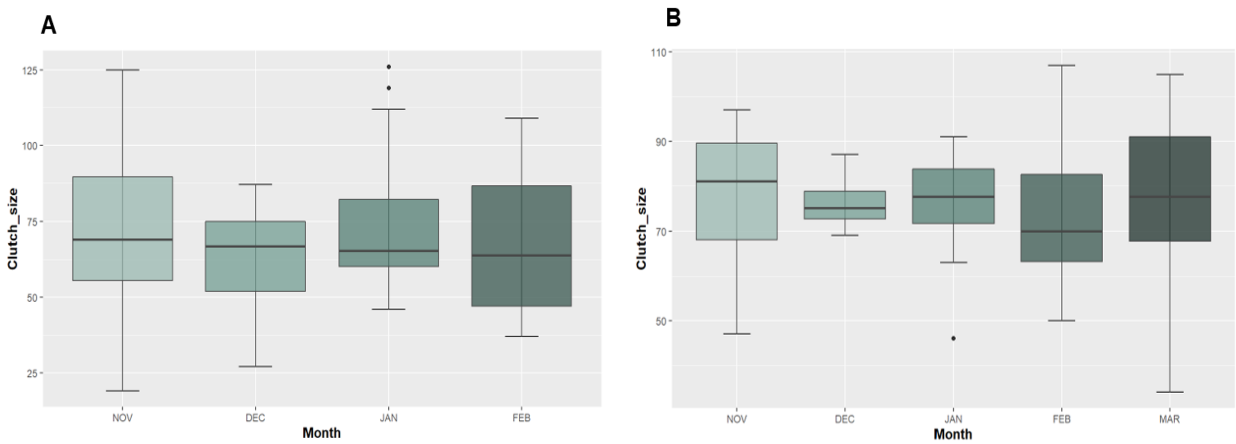

Figure 26. Distribution of the clutch size per month in the seasons 2021-2022 (A) and 2022-2023 (B).

3.5.3. RELATIONSHIP BETWEEN CLUTH SIZE AND FEMALES BODY SIZE

For the season 2021–2022, there was a positive correlation between CCW and clutch size ($R^2 = 0.1363$, t value = 2.809, P<0,01). For the season 2022–2023, both CCL and CCW were correlated with the number of eggs released by a female turtle (clutch size) ($R^2 = 0.116$, t value = 2.461, P<0,01; $R^2 = 0.176$, t value = 3.137, P<0,01), with a bigger clutch size for higher CCL and CCW (Figure 13).

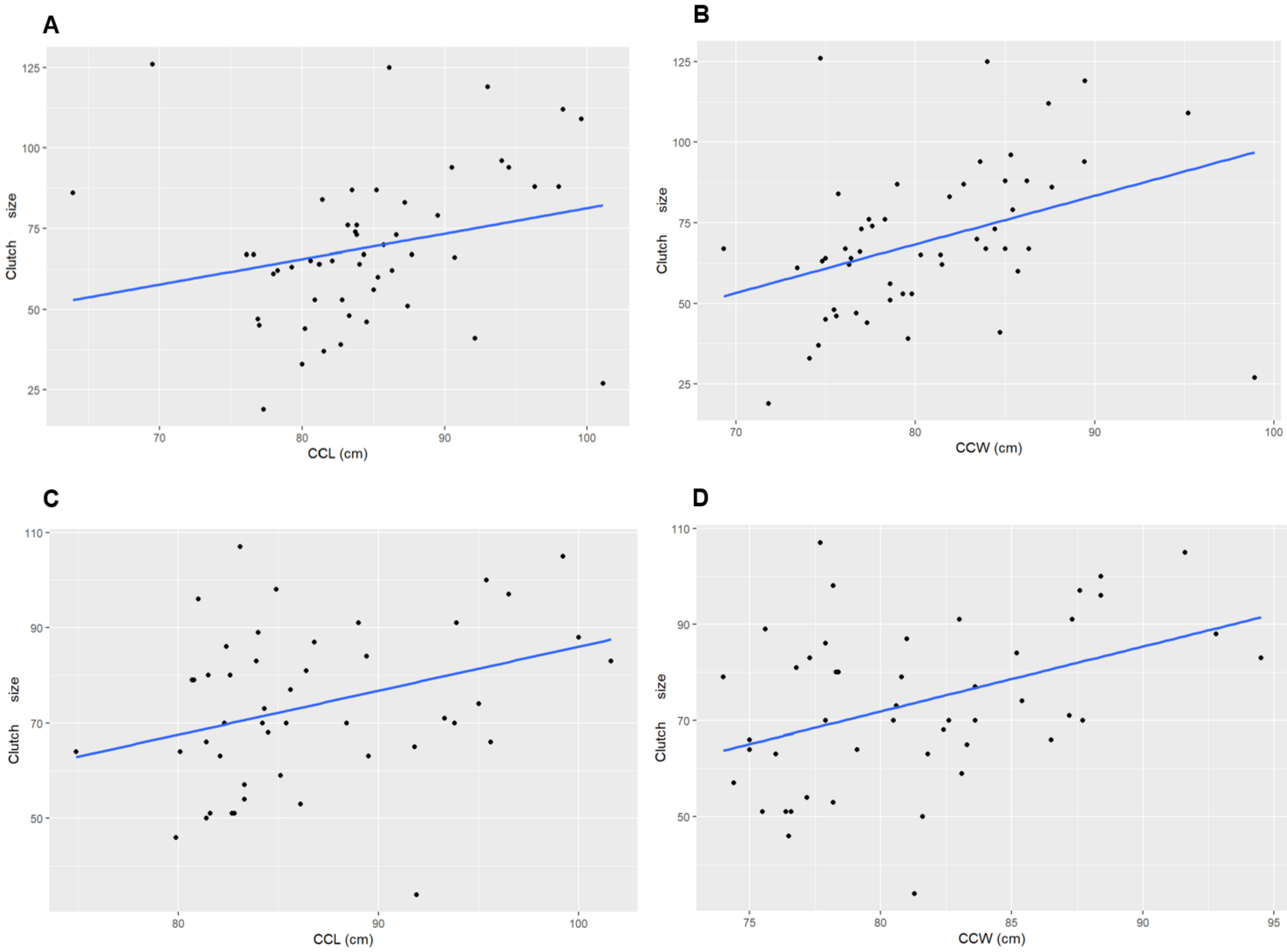

Figure 27. Correlation between the CCL and the CCW with the clutch size recorded during the seasons 2021-2022 (A), (B) and 2022-2023 (C), (D).

3.6. MARKED TURTLES AND RECAPTURES

A total of 119 nesting green turtles were marked during the full study seasons: 65 during the season 2021–2022, and 54 during the season 2022-2023. During the first studied season, 34 turtles were recaptured, and 28 during the second. From the turtles recaptured during the season 2022–2023, just two of them were marked during the previous season, while the others were marked during the same season.

The observed internesting period (OIP) and the estimated clutch frequency (OCF) (mean ± SD) were 12.643 ± 2.341 and 2.574 ± 1.220, respectively, in the season 2021–2022, and 12.267 ± 2.314 and 2.558 ± 1.104 in the season 2022–2023. Neither for the OIP nor for the OCF there were significant differences between the two studied seasons (n = 29, F value = 0.189, P = 0.667; n=60, F value = 0.03, P = 0.957).

3.7. NESTS

3.7.1. HATCHING SUCCES, EMERGING SUCCESS AND FERTILITY

Table 3 shows the hatching success, emerging success, and fertility (mean ± SD) obtained from the data collected during the nest exhumations on Pejeperro and Rio Oro beaches during the seasons 2021-2022 and 2022-2023.

There were no significant differences in the means of hatching success (F value =0.279, P = 0.598), emerging success (F value = 0.07, P = 0.792), and fertility (F value = 1.541, P = 0.216) between the seasons 2021–2022 and 2022–2023.

Moreover, in any of the two studied seasons, there weren’t significant differences in the means of hatching success (F value = 1.785, P = 0.184 for season 2021-2022 and F value = 0.420, P = 0.519 for season 2022-2023), and the means of emerging success (F value = 0.671, P = 0.425 for season 2021-2022; F value = 0.148, P = 0.701 for season 2022-2023) between Pejeperro and Rio Oro beaches.

Table 3. Hatching success, emerging success and fertility obtained during seasons 2021-2022 and 2022-2023 on the two monitored beaches.

SEASON	***BEACH***	***N***	***HATCHING SUCCESS (%)***	***EMERGING SUCCESS (%)***	***FERTILITY (%)***
2021-2022	***PP***	59	84.751 ± 17.854	79.516 ± 27.789	88.389 ± 14.962
	RO	59	88.690 ± 13.933	83.204 ± 20.609	91.119 ± 12.820
	TOTAL	**118**	**86.721 ± 16.067**	**81.360 ± 24.427**	**89.754 ± 13.940**
2022-2023	***PP***	34	87.100 ± 26.242	83.748 ± 30.252	91.663 ± 20.556
	RO	30	82.692 ± 28.145	80.938 ± 27.757	93.734 ± 10.907
	TOTAL	**64**	**85.034 ± 27.023**	**82.431 ± 28.914**	**92.634 ± 16.649**

Moreover, Table 4 includes the hatching success, emerging success, and fertility (mean ± SD) of the nests exhumed in beach zones 2 and 3 for each of the seasons.

Table 4. Hatching success and emerging success of the nests located in zones 2 and 3 and which were exhumed during seasons 2021–2022 and 2022–2023.

SEASON	***ZONE***	***N***	***HATCHING SUCCESS***	***EMERGING SUCCESS***
2021-2022	***2***	42	83.112 ± 18.556	73.960 ± 33.222
	3	75	88.790 ± 14.170	85.602 ± 16.338
2022-2023	***2***	26	71.788 ± 36.137	70.269 ± 35.728
	3	38	94.096 ± 12.387	90.752 ± 27.19.645

In the season 2022–2023, the beach zone in which the turtle laid the eggs had a significant effect on the hatching success and the emerging success. The hatching success and emerging success of the nests located in zone 3 were significantly higher than those situated in zone 2 (F value = 12.429, P<0,001 for hatching success; F value = 8,694, P<0.001 for emerging success).

On the other hand, in the season 2021–2022, there were no significant differences in hatching success and emerging success between the nests located in zone 2 and zone 3 (F value = 3.4853, P = 0.064; F value = 6.502, P = 0.012).

3.7.2. FERTILITY OVER TIME

Considering the seasons 2021-2022 and 2022-2023, for none of them, there were significant differences in fertility as months went by throughout the season (n = 118, F value = 1.218, P = 0.303; n = 64, F value = 0.594, P = 0.758).

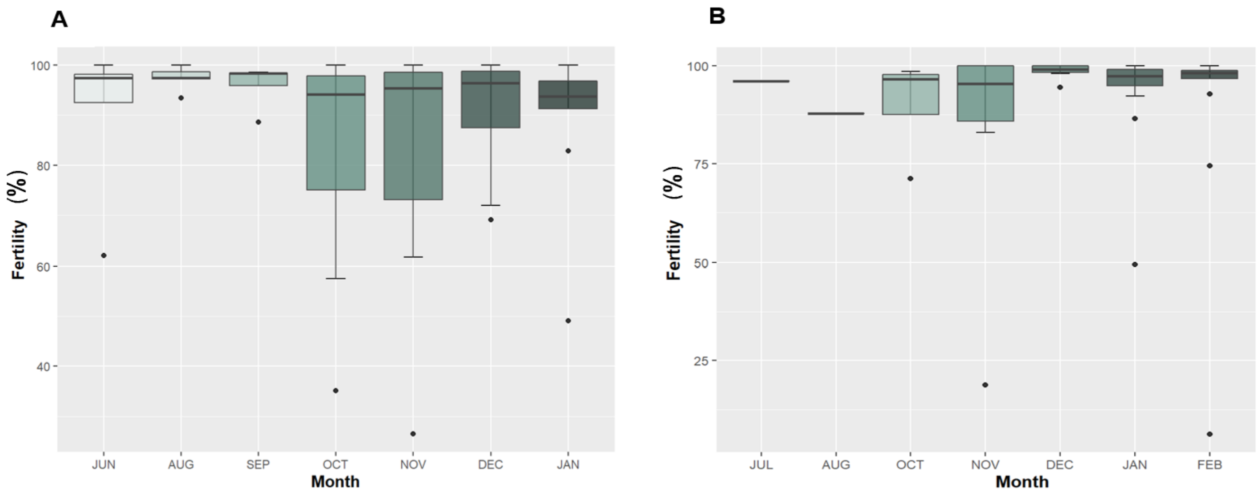

Figure 28. Fertility per month in the seasons 2021-2022 (A) and 2022-2023 (B).

4. DISCUSSION

Green Turtles are widely geographically distributed in areas with similar environmental characteristics, taking in consideration specially the climate, the temperature, and the precipitation (Pike, 2013).

Pejeperro and Rio Oro beaches are located in a tropical region, on the south Pacific coast of Costa Rica. The environmental conditions there, the ecosystems that surround them, their remote location, the soft sediments, and the extensive and exposed beach habitat provide critical nesting habitat for the Pacific green turtle

(Chelonia Mydas) (Quesada-Alpíza & Cortes, 2006; C. R. I., 2013; Friedlander et al., 2022).

Because of the physical and environmental similarities between Pejeperro and Rio Oro beaches (Friedlander et al., 2022; Sellés-Ríos et al., 2022), there were no significant differences in the total nesting activity (considering the confirmed nests and the false crawls) between the two studied beaches during the seasons 2021-2022 and 2022-2023, and neither did the turtles had a preference for nesting on one of the two beaches. For the same reason, no differences in hatching success, emerging success, and fertility were observed between the two beaches in any of the two seasons studied.

The total nesting success rates were 20.33% in the season 2021-2022 and 30.65% in the season 2022-2023. The nesting success, and therefore, the number of confirmed nests, was higher during the season 2022–2023. There are some factors that can affect nesting success, such as artificial lights, the presence of obstacles, shadows, and movements from animals and people present at the beach, and the physical and chemical characteristics of the beach sand (Ekanayake et al., 2011; Hamann et al., 2021). Greater nesting success can be found on well-ventilated substrates with low salinity and high humidity (Ekanayake et al., 2011). In addition, previous studies have reported relationships between weather and nesting success, with higher nesting success with increased sand moisture or rainfall and lower nesting success with elevated daytime temperatures (Hamann et al., 2021). Between December 2022 and February 2023, there were lower temperatures than normal in the North Pacific, Central Pacific, and South Pacific of Costa Rica (Pronóstico climático, IMN, s. f.), which could have contributed to the enhancement of nesting success during the season 2022-2023. Furthermore, an improvement in the patrol and conservation efforts during the season 2022-2023 in order to manage to have fewer people, such as fishermen, moving around the main nesting parts of the beaches and using artificial lights probably also led to a higher nesting success. An interannual variation in green turtle nesting has also been observed at other nesting beaches, including Tortuguero, in the Caribbean part of Costa Rica (Whiting et al.,2014), Raine Island in Australia (Hamann et al., 2021), and the Cayman Islands (Bell et al., 2007), among others.

Green turtle nesting was seasonal for both studied seasons. The nesting season lasted about 5 months, between October and March, with a more pronounced peak between December and February, which coincides with the warm and dry season in this region. Similar patterns have been reported at Playa Cabuyal, Gulf of Papagayo, in the East Pacific of Costa Rica (Santidrian et al., 2015); at Tortuguero, in the Caribbean part of Costa Rica (Troëng & Rankin, 2005; Troëng & Chaloupka, 2007); at Ascension Island in the South Atlantic (Godley et al., 2021); and at Mayotte Island in the southwest Indian Ocean (Bourjea et al., 2007). It has been speculated that seasonal nesting occurs at times of the year with climatic conditions that maximize reproductive fitness (Ekanayake et al., 2013). The temperature and humidity during the months with the maximum nest activity in this region seem to favour the development of embryos in the nest (Zavaleta-Lizárraga & Morales-Mávil, 2013). High atmospheric pressure, which results in warmer and drier weather typical for the dry season, favours green turtle nesting (Palomino-González et al., 2020), while clutches are negatively affected by intense rainfall (Balladares et al., 2022).

Most of the green turtle (Chelonia Mydas) nests on Pejeperro and Rio Oro beaches were placed in zone 3, while the majority of false crawls happened in zone 2. The exact same trend has been reported at Playa Cabuyal, Gulf of Papagayo, in the East Pacific of Costa Rica (Saura et al., 2022; Santidrian et al., 2015). Furthermore, in the season 2022-2023, the hatching success and emerging success of the nests located in zone 3 were significantly higher than those situated in zone 2. Green turtle females carry out a complex nesting site selection, laying the eggs in zones with favourable characteristics for embryonic development (Zavaleta-Lizárraga & Morales-Mávil, 2013). There are many factors that can have an impact on nest site selection, including distance to the water, risk of erosion and tidal inundation of nests, risk of depredation, elevation, slope, presence of vegetation, sand grain size, sand moisture, and temperature, among others (Santos et al., 2015; Santidrian et al., 2015). In Zone 3, there is vegetation with a substrate made up of fine and moist sands, which avoids egg desiccation (Zavaleta-Lizárraga & Morales-Mávil, 2013), the probability of erosion and tidal inundation as well as depredation of nests laid is lower (Patrício et al., 2018; Santidrian et al., 2015), there is a slightly higher elevation, which prevents clutch flooding due to SLR and storm events (Patrício et al., 2018), and there is high vegetation coverage, which increases shade and lowers the incubation temperature of developing eggs (Santidrian et al., 2015). In previous studies, it has also been proven that the proportion of eggs hatching, and neonates' nest emergence decreases at higher incubation temperatures (Weber et al., 2012). Moreover, sea turtles are species with temperature-dependent sex determination, which makes them particularly vulnerable to climate change as further warming could result in extremely biased sex ratios or offspring of only one sex (Saura et al., 2022). Using the vegetation zone as a preferred nesting site can mitigate the temperature-linked impacts on the sex ratio and on hatching and emerging success (Patrício et al., 2018). Therefore, some important characteristics of zone 3 promote an increased rate of offspring survival and allow a possible adaptation against climate change and global warming (Patrício et al., 2018; Saura et al., 2022).

Regarding the horizontal distribution, on Pejeperro Beach, most of the nests were placed from sectors 80 to 84 and from sectors 86 to 89. Sector 85 presented a lower number of confirmed nests and more false crawls. In the sectors situated next to the Rio Oro's River mouth and next to the Pejeperro coastal lagoon, there was just the presence of false crawls. On the Rio Oro beach, the area with the highest nesting activity and the largest number of confirmed nests was concentrated from sector 63 to sector 73. The sectors that were situated close to the Pejeperrito Coastal Lagoon and the Rio Oro's River mouth were the ones with the fewest confirmed nests, having almost only false crawls. For both beaches, the sectors with more confirmed nests were the ones with more vegetation density. In the sectors close to Rio Oro's River mouth and the two coastal lagoons, there wasn't vegetation. In addition, in sector 85, the vegetation density was considerably lower compared to the other sectors. Thus, it was assumed that female turtles had a preference to nest in sectors with high vegetation coverage, whereas they almost never lay eggs in sectors without or with low vegetation.

For the two studied seasons, moon phases had a clear effect on the green turtle emerging with the purpose of nesting on both beaches. Recent studies also found a nesting pattern by sea turtle species related to the lunar cycle (Barik et al., 2014; Dornfeld et al., 2015). This relationship between lunar phases and nesting activity could be related to the portion of the moon that is illuminated, which could affect nesting sea turtle visuality, but also to the tidal cycles, which are also linked to the lunar cycle (Law et al., 2010; Naylor, 1999; Pike, 2008). On Pejeperro and Rio Oro beaches, there were a higher number of female emergencies during the nights with first and last quarter moons in comparison with the nights with full and new moons. On clear nights with a full moon, there is better visibility for predators, and the presence of people or objects on the beach is easier to perceive, which may discourage turtles from emerging (Law et al., 2010). On the other hand, on darker nights with the new moon, artificial light and dark silhouettes are more visible, which also prevent turtles from emerging (Law et al., 2010). In addition, at nights with full and new moons, tidal cycles reach their extremes, which negatively influence green turtle nesting (Palomino-González et al., 2020).

The body sizes, CCL and CCW, from green turtles that nested in Pejeperro and Rio Oro beaches were similar to the ones from East Pacific green turtles that nest at Playa Cabuyal, Gulf of Papagayo, in the Northern Pacific part of Costa Rica (Santidrian et al., 2015), but they were lower than those from green turtles from other ocean basins, as stated in previous reports (Hirth, 1997).

Compared with other populations of green turtles, this population of Pacific turtles exhibited smaller clutch sizes (mean ± SD): 69 ± 23 for the season 2021-2022 and 75 ± 16 for the season 2022-2023 (Santidrian et al., 2015).

The number of eggs increased with the size of the turtle (CCL and CCW). This finding is in accordance with other studies that have shown that clutch size increases with female body size in sea turtles (Gouvello et al., 2020; LeBlanc et al., 2014; Santidrian et al., 2015). It supports the Optimal Egg Size Theory, which states that nesting turtles maximize clutch size as a response to the high mortality at early life stages (Gouvello et al., 2020).

Capture−mark−recapture of nesting turtles at Pejeperro and Rio Oro beaches indicated that females laid an average of 2.574 ± 1.220 clutches per nesting season (OCF) in the season 2021-2022, and 2.558 ± 1.104 in the season 2022–2023. The number of days between those clutches (OIP) (mean ± SD) was 12.643 ± 2.341 in the season 2021-2022 and 12.267 ± 2.314 in the season 2022–2023. The observed clutch frequency (OCF) and the observed interesting period fell within the upper limit reported for green turtles (Santidrian et al., 2015).

No significant differences in clutch size and fertility were observed as months went by throughout the season. This doesn't match with previous studies, which demonstrated that clutch size and fertility in some sea turtle species decrease as the nesting season progresses due to maternal body fat reserves being depleted later in the season (Gouvello et al., 2020; LeBlanc et al., 2014).

5. CONCLUSIONS

In conclusion, this study has provided valuable insights into the nesting ecology of the Pacific green turtle (Chelonia mydas) in the South Pacific of Costa Rica. By analysing several aspects of the nesting process, including nesting success, the temporal and spatial distribution of the nesting activity, nest site selection, female biometrics and reproductive output, and hatching and emerging success, we have gained a better understanding of the reproductive behaviour and ecological requirements of this endangered species in this region.

The study showed that nesting success is influenced by various factors, including beach characteristics, environmental conditions, vegetation coverage, and human disturbances. Identifying and mitigating the main threats and enhancing the patrol efforts is crucial for maintaining suitable nesting environments and improving nesting success rates.

Our findings indicate that green turtles have a strong preference to nest in sectors with higher vegetation density. In addition, they carry out a complex nest site selection, choosing appropriate beach zones to nest where the environmental, chemical, and physical characteristics, as well as other distinctive zone particularities, ensure a successful incubation and emergence of hatchlings. Likewise, they have a seasonal nesting pattern in which the nesting peak period corresponds to those months in which the environmental conditions benefit the development of the embryos. This behaviour points up the importance of conserving and protecting these beach zones to ensure the long-term survival of green turtle populations. Moreover, the complex nest site selection and seasonal nesting behaviour of the green turtle demonstrate remarkable adaptation abilities which are important for the constant and critical changings of the environment.

Moon phases play a significant role in sea turtle emergencies. The presence or absence of moonlight and tides influence nesting activity during the night. Generally, nights with first quarter and last quarter moons result in higher nesting attempts than nights with full and new moons. This is of special interest as patrol and conservation efforts can be focused, improved, and optimized at night with the moon phases, which results in more nesting activity. However, more research is needed to explore the specific impacts of moon phases on sea turtle emergencies.

The analysis of clutch size variation revealed interesting relationships with the female body size, with larger turtles generally producing more eggs per clutch as strategy to optimize their fitness. This finding highlights the importance of protecting adult females, as they play a critical role in maintaining population levels.

Overall, our research contributes to a wider understanding of the nesting ecology of the Pacific green turtles in the South Pacific of Costa Rica and emphasizes the need for effective conservation measures. By implementing and improving conservation strategies such as beach patrolling, habitat restoration, and sustainable management practices, we can safeguard the nesting habitats and support the recovery of green turtle populations.

Further investigations should focus on a deeper understanding of which and how environmental conditions play a fundamental role in the nesting and reproductive behaviour as well as study new environmental, physical, climate and oceanographic processes and conditions that can also have a direct or indirect effect on these aspects. Expanding our understanding of the interconnection of the nesting process with the foraging and migratory behaviours could be interesting to integrate both nesting and unnesting phases of the green turtle's life cycle in order to develop comprehensive conservation strategies that promote the overall well-being and persistence of this remarkable species.

It is also important to consider the need for collaborative efforts among scientists, conservation organizations, and local communities to protect and conserve this species. By combining research, education, and sustainable practices, we can ensure a brighter future for these iconic creatures and the ecosystems they inhabit.

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