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ORIGINAL PAPER

# Inter-beach movements and inter-nesting periods of olive ridley sea turtles relate to nesting behavior in a nascent arribada beach

Roger Fusté[1,2] · Carmen Mejías-Balsalobre[1,3] · Emily G. Webster[1,4] · Isabel Naranjo[1] · Randall Arauz[1,5] · Daniela Rojas-Cañizales[1,6,7]

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## Abstract

Olive ridley sea turtles (*Lepidochelys olivacea*) exhibit two nesting behaviors: solitary nesting and synchronized mass-nesting, known as *arribada*, with females able to switch between behaviors rather than being exclusive to one strategy. Although arribadas are thought to be driven by environmental and/or social cues that promote synchronized breeding, it remains unclear to what extent they can shape the spatial and temporal dynamics of nesting olive ridleys. Our study documents how nesting behavior influences the frequency of inter-beach movements and the length of within-season inter-nesting periods (IP). We examined records of 4,273 tagged and 555 recaptured individuals from 2016 to 2019 at Corozalito, a nascent arribada nesting beach on the Costa Rican Pacific, and its three neighboring solitary-nesting beaches. Inter-beach movements were recorded for 99 turtles (17.8%), primarily from solitary-nesting beaches towards Corozalito during arribadas. IPs of females nesting in arribadas were not consistent across seasons while IPs between consecutive solitary nesting events were stable across years and comparable to values reported for other olive ridley rookeries. We suggest that arribadas at Corozalito prompt inter-beach movements of olive ridleys that nest on solitary neighboring beaches, attracting them to the mass nesting location. Additionally, breeding synchrony may extend the IP of turtles that have already laid their first nest by delaying oviposition until the arribada begins. However, this delay appears to be context-dependent, likely influenced by the timing of arribadas and individual nesting histories. These findings contribute to better understanding the processes involved in the formation of arribadas and their associated nesting dynamics.

**Keywords** Mass nesting event · *Lepidochelys olivacea* · Eastern Tropical Pacific · Solitary nesting · Nest site fidelity · Nesting synchrony

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✉ Roger Fusté
rogerfusteimach@gmail.com

Carmen Mejías-Balsalobre
cmejiasbal@riama.org

Emily G. Webster
emily.webster1@jcu.edu.au

Isabel Naranjo
inaranjo@cremacr.org

Randall Arauz
randridley@gmail.com

Daniela Rojas-Cañizales
danielarojas159@gmail.com

[1] Rescue Center for Endangered Marine Species (CREMA), San Francisco de Coyote, Costa Rica

[2] Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain

[3] Red de Investigadores Actuando por el Medio Ambiente (RIAMA), Madrid, Spain

[4] James Cook University, Townsville, Australia

[5] Marine Watch International, San Francisco, USA

[6] Grupo de Trabajo en Tortugas Marinas del Golfo de Venezuela (GTTM-GV), Maracaibo, Venezuela

[7] School of Natural Resources and Environment (SNRE), University of Florida, Gainesville, USA

## Introduction

Breeding synchrony confers a survival advantage to many plant and animal taxa, by diluting predation risk when organisms reproduce en masse (Hamilton 1971; Ims 1990). Among vertebrates, one well-known example is the olive ridley sea turtle (*Lepidochelys olivacea*, Eschscholtz, 1829), which nests in synchronized mass aggregations of thousands of individuals, known as arribadas (Srikanthan et al. 2024; Valverde et al. 2012). Arribadas are relatively uncommon events restricted at specific rookeries in the eastern Pacific, the western Atlantic, and the northern Indian Ocean, and represent a unique reproductive behavior among sea turtles characteristic of the genus *Lepidochelys* (Bernardo and Plotkin 2007). The frequency and temporal patterns of arribadas can vary among rookeries. For example, at Ostional (Costa Rica), synchronic nesting events occur with near-monthly regularity (Valverde et al. 2012), whereas at Gahirmatha and Rushikulya (India) they are typically restricted to a single annual event during the dry season (Shanker et al. 2004). In contrast, at Nancite and Corozalito (Costa Rica), arribadas occur intermittently during the rainy season (Fonseca et al. 2023; Rojas-Cañizales et al. 2022). These contrasting patterns highlight strong location-specific phenologies and suggest that the mechanisms driving nesting synchrony in olive ridleys vary across regions and seasons rather than being universal.

Breeding synchrony, however, is not the only nesting strategy displayed by the species, as female olive ridleys may also nest in solitary (i.e. alone or in small non-synchronic groups) (Bernardo and Plotkin 2007). In fact, while arribadas are restricted at specific beaches, solitary nesting occurs throughout the species' geographic range (Bernardo and Plotkin 2007; Honarvar et al. 2016; Pandav et al. 1998; Plot et al. 2012). Even at the rookeries where arribadas take place, females nest in solitary between mass nesting events (Hughes and Richard 1974; Kalb 1999; Plotkin et al. 1995). Moreover, several studies have shown that female olive ridley can exhibit both nesting strategies within a single location and season or move from a solitary nesting site to participate in an arribada, resulting in mixed nesting behaviors (Fonseca et al. 2014; Kalb 1999; Plotkin 2002; Pritchard 2007; Rojas-Cañizales et al. 2022; Ruthig and Gramera 2019). Such behavioral flexibility may be linked to the variable timing and frequency of arribadas and suggests that the selection of the nesting strategy plays a key role in shaping the spatial and temporal patterns of olive ridleys (Kalb 1999; Dornfeld et al. 2014).

Olive ridleys, like most sea turtles, exhibit some degree of nest site fidelity, with individuals tending to return to nest at the same locations both within and between nesting seasons (Dornfeld et al. 2014; Matos et al. 2012; Miller 1997; Tripathy and Pandav 2007). Females nest annually and typically lay two clutches per season (Bernardo and Plotkin 2007; de Castilhos et al. 2022; Kalb 1999; Williamson et al. 2019), which are usually separated by two to four weeks (Dornfeld et al. 2015; Hancock et al. 2019; Matos et al. 2012; Maxwell et al. 2011). This interval between consecutive nesting events within a season is known as the inter-nesting period (IP) (Alvarado and Murphy 1999). Both nest site fidelity and IP have been suggested to differ in olive ridleys according to nesting behavior.

At the mass nesting beach of Nancite, Kalb (1999) found that arribada nesters (defined as females whose first nesting event of the season was detected in an arribada), exhibited a strong nest site fidelity, returning to the same rookery during subsequent arribadas within the same season. In contrast, solitary nesters (defined as females whose first event of the season was in solitary) were more likely to shift locations, nesting in either solitary or arribadas. Two non-exclusive mechanisms may explain these differences. First, females from nearby waters may respond to the cues that trigger the onset of arribadas. Mass nesting events have been suggested to be conditional on external cues, such as onshore winds, precipitation, lunar and/or tidal cycles, currents, sea level pressure, chemical signaling or social facilitation (Barik et al. 2014; Bézy 2019; Bézy et al. 2020; Coria-Monter and Durán-Campos 2019; Srikanthan et al. 2024). However, the spatial extent over which these cues may operate remains unknown. Second, pre-nesting spatial behavior in front of mass nesting locations could also help explain this different pattern across nesting behaviors, as olive ridleys form dense offshore aggregations in front of arribada rookeries (Cornelius 1986; Kalb 1999; Behera et al. 2010; Tripathy 2013; Bezy 2019). The processes underlying the formation of these aggregations remain poorly understood, including the biotic and abiotic factors involved, and the temporal and spatial scales at which they operate (Rao et al. 2023; Shanker 2021). In some regions, offshore aggregations have been observed months before the onset of arribadas and even during years when mass nesting does not occur (Rao et al. 2023), suggesting that aggregation formation and the initiation of the mass nesting event may be driven by independent processes. Thus, although the underlying mechanisms remain unknown, documented inter-beach movements toward arribada rookeries (Rojas-Cañizales et al. 2022) may reflect solitary nesters joining these offshore aggregations or responding to the cues that trigger arribadas.

Kalb (1999) also reported longer IPs in arribada nesters, compared to solitary nesters. Olive ridleys are known for their capacity to delay oviposition, an ability which could facilitate breeding synchrony or ensure environmental conditions are favorable for nesting (Plotkin et al. 1997; Rostal et al. 1998). By delaying oviposition to nest in an arribada, individuals increase their fitness through increased hatching success via predator satiation, as nests laid in solitary experience a much higher predation rate (Eckrich and Owens 1995; Bernardo and Plotkin 2007). Therefore females could remain in the vicinity of the nesting beach until the onset of the next synchronic nesting event (Plot et al. 2012), lengthening their inter-nesting period (IP) in those cases were they have already laid its first nest of the season. With the exception of Kalb (1999), these patterns have rarely been examined. Thus further research is warranted into arribada timing, possible cues to aggregate or to set the beginning of the mass nesting event, and how these interact with individuals' nesting cycles to shape spatial and temporal dynamics of olive ridley nesting.

Corozalito is nascent arribada nesting beach in the Pacific of Costa Rica, hosting over 2,000 successful solitary nesting events (i.e., individual nests not associated with an arribada) and between one to five arribadas per nesting season (Rojas-Cañizales et al. 2022; Espinoza-Rodriguez et al. 2023). At this site, arribadas were first detected in the early 2000s and since then, have been increasing in frequency and size (Mejías-Balsalobre et al. 2024; Rojas-Cañizales et al. 2022). In addition to Corozalito, three neighboring nesting beaches, at which only solitary nesting events take place, are located within 15 km of the mass nesting location (Binhammer et al. 2019; Espinoza-Rodriguez et al. 2023; Viejobueno et al. 2011). This spatial configuration provides a valuable opportunity to examine how nesting behaviors influence the temporal and spatial reproductive dynamics of female olive ridleys. Using a metal tagging approach to monitor individual females across nesting events, we aim to: (1) quantify the frequency of inter-beach movements between Corozalito and its neighboring solitary nesting beaches, assessing whether the occurrence of arribada events is associated with increased movements from nearby locations and (2) examine the relationship between nesting strategy (arribada, solitary or combination of both nesting behaviors) and IP at Corozalito.

## Methods

Corozalito (9°50′55.40″ N; 85°22′47.67″ W) is a 768 m-long beach located on the Southern Nicoya Peninsula, on Costa Rica's Pacific coast (Fig. 1a) (Rojas-Cañizales et al. 2022; Mejías-Balsalobre et al. 2024). This area of the Pacific coast exhibits two distinct climatic seasons: a dry season from December to June and a rainy season from July to November (Bernardo and Plotkin 2007; Dornfeld et al., 2014), with olive ridley nesting activity occurring primarily between June and December (Reavis et al. 2022; Espinoza-Rodriguez et al. 2023). At Corozalito, arribadas usually occur from August to January, lasting from one to five days and with the largest reported event involving as many as 21,653 laying turtles (Rojas-Cañizales et al. 2022). Corozalito´s nesting activity has been monitored uninterruptedly since 2008 by the Rescue Center for Endangered Marine Species (CREMA), which also monitors its three neighboring solitary nesting beaches (Espinoza-Rodriguez et al. 2023; Mejías-Balsalobre et al. 2024). From north to south, these beaches are Bejuco (BE, 3.5 km long), San Miguel (SM, 2.5 km long), and Costa de Oro (CDO, 4.6 km long), with

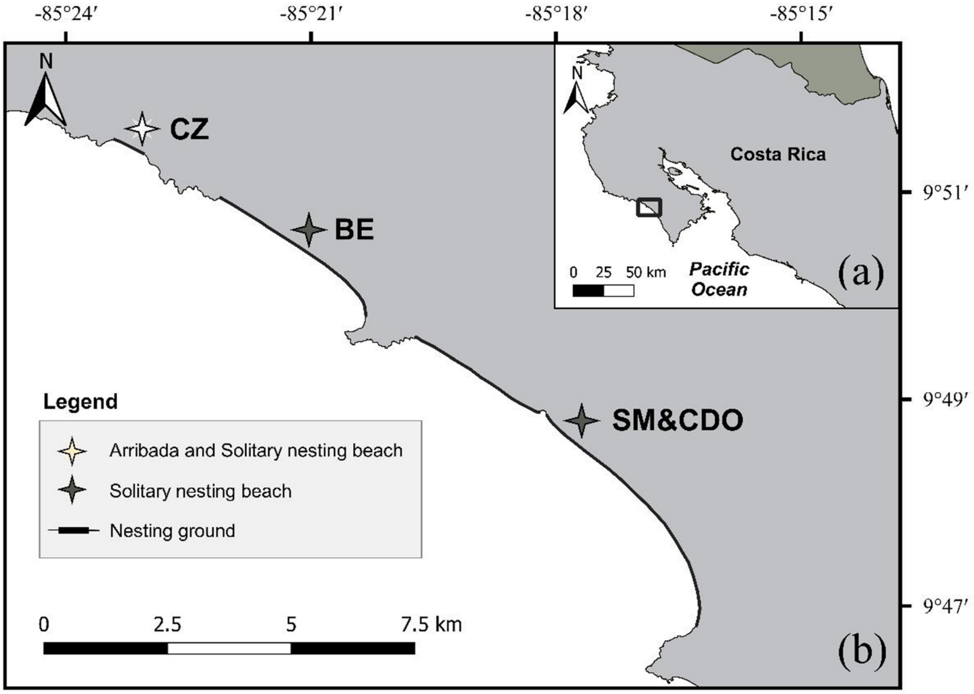

**Fig. 1** (**a**) Geographical location of the study area in the Southern Nicoya Peninsula, Costa Rica (black rectangle) and, (**b**) Detailed map of the surveyed nesting beaches from north to south: Corozalito (CZ), Bejuco (BE), and San Miguel and Costa de Oro (SM&CDO)

BE being the closest to Corazolito, at 1.5 km and CDO the farthest at 15 km away (Reavis et al. 2022; Viejobueno et al. 2011). For this study we considered SM and CDO as the same nesting beach (SM&CDO), as they are only separated by a small estuary and it is possible to cross from one to another by foot during low tide, while the other rookeries are separated by rocky outcrops (Beange 2018, Reavis et al. 2022) (Fig. 1b).

## Data collection

Between 2016 and 2019, nightly patrols were conducted from July to January to record nesting activity at each location (Reavis et al. 2022; Rojas-Cañizales et al. 2022). During these patrols, nesting sea turtles were actively searched for along the beach. For each nesting event encountered, we recorded the date, location, time, and status of the nesting event (successful/unsuccessful) (Reavis et al. 2022). Untagged turtles were marked with Inconel flipper tags (Style 681, National Band and Tag Company) using a standard applicator on the second-most proximal scale of the fore flipper (Dornfeld et al. 2014; Matos et al. 2012), whereas for previously tagged turtles, we recorded the tag number and any additional information inscribed on the back of the tag (Rojas-Cañizales et al. 2022).

As described by Rojas-Cañizales et al. (2022), we considered the start of an arribada at Corozalito to be when 50 or more females were simultaneously ovipositing regardless of the total number of turtles present on the beach (e.g., digging nests, ovipositing, emerging or returning to the sea). Nesting was classified as solitary unless this threshold was reached. This criterion is consistent with methods used at other arribada nesting locations (Valverde and Gates 1999), given that no formal guidelines have been established to determine the onset of arribadas. Based on previous records of olive ridley nesting activity at this rookery, reaching this threshold is typically followed by an increase in the number of females on the beach in subsequent hours (unpublished data). Importantly, this definition of arribada is operational and does not infer when environmental and biological mechanisms begin to influence nesting females. Rather, it provides a consistent and field-applicable criterion for distinguishing solitary from mass-nesting events. Once the arribada was considered to have started, priority was given to actively searching for and recording previously tagged turtles, while tagging of unmarked individuals was primarily conducted at the peak of the mass nesting event (Beange et al. 2018).

## Data analysis

We classified recaptures (encounters with previously tagged females) into two categories depending on whether the female's previous encounter occurred within the same nesting season (renesting) or during a previous nesting season (remigrant) (Carr and Carr 1972; Dodd 1983). Although criteria were established to define the onset of arribadas at Corozalito, distinguishing between mass and solitary nesting remains challenging because nesting density often increases and declines gradually (Cornelius and Robinson 1985). To minimize potential misclassification during transitional periods, individuals nesting during the three nights preceding an arribada or on the first night following an arribada were not classified as solitary nesters (Cornelius and Robinson 1985). Instead, these were categorized as intermediate nesting events (Kalb 1999) and were excluded from subsequent analyses.

### Inter-beach movements

We defined the inter-beach movements as instances where a tagged turtle was observed emerging on a different beach than where it had been previously recorded nesting (Tripathy and Pandav 2007). Movements were classified according to the origin and destination nesting beach, and the nesting behavior displayed (solitary/arribada). The origin beach was defined as the location of the immediately preceding nesting event and the destination beach as the location of the subsequent nesting event (Rojas-Cañizales et al. 2022). Lastly, we classified movements into intra-seasonal, if both sightings occurred within the same season, or inter-seasonal if they occurred in different seasons (Tripathy and Pandav 2007).

We constructed Generalized Linear Models (GLM) with a Poisson distribution to (1) evaluate whether arribada events at Corozalito influenced inter-beach movements from the neighboring nesting locations and (2) to compare if the frequency of movements in solitary differed across the three nesting locations. We did not consider inter-seasonal beach movements for the analysis, since it was not possible to determine whether the movement occurred within the same season the turtle was detected at the destination beach or if it had occurred prior to that season, and the movement was not detected.

The study followed a nested factorial design, as arribadas occurred at only one of the three studied locations (Schielzeth and Nakagawa 2013). Therefore, because nesting behavior and location were not fully crossed and were perfectly confounded, their effects could not be estimated simultaneously within a single model. Consequently, two separate models were fitted. First, we fitted a model to determine whether movements from the solitary nesting beaches towards Corozalito were more frequent during arribadas than during solitary events. In this model, the response variable was the number of movements from solitary nesting

**Table 1** Classification and categories of the inter-nesting period (IP) according to the nesting behavior (solitary and arribada)

| Nesting categories | Nesting description |
|---|---|
| Arribada-Arribada (AA) | Arribada in both encounters |
| Solitary-Solitary (SS) | Solitary in both encounters |
| Arribada-Solitary (AS) | Arribada on the first encounter and solitary on the second encounter |
| Solitary-Arribada (SA) | Solitary on the first encounter and arribada on the second encounter |

at the origin beach (BE or SM&CDO) towards either solitary or arribada nesting at Corozalito within a given season. Explanatory variables included the nesting behavior at Corazolito, the original beach and the nesting season. The total number of movements within each season was included as an offset to weight the response variable. Secondly, we fitted a separate model to compare the number of inter-beach movements occurring only between successive solitary events among beaches (BE, SM&CDO and CZ). The explanatory variables included the origin beach, destination beach and nesting season. The total number of movements between successive solitary events within each season was used as an offset.

### Inter-nesting period

We calculated the IPs for those tagged individuals that successfully laid two consecutive nests within a season (Dornfeld et al.2014). IPs were classified into four categories based on the nesting behavior exhibited in the two encounters (solitary or arribada) (Table 1). IPs longer than 66 days were excluded and considered multiple IPs, as this duration exceeds the maximum reported for olive ridleys (Plotkin et al. 1995). Similarly, IPs shorter than 6 days were not considered, as sea turtles are physiologically incapable of laying two clutches within this period (Miller 1997).

We performed a Kruskall-Wallis test to examine whether IP differed among nesting behaviors and seasons. For the analysis, IP was treated as the response variable, with the nesting behavior and season included as predictors. Finally, we conducted Dunn's post hoc test with Holm-Bonferroni adjustment to account for multiple comparisons.

## Results

During the four nesting seasons, we tagged a total of 4,273 female olive ridleys. Most turtles were tagged at Corozalito (*n*=2,255), including 1,168 nesting in solitary, 953 during arribadas and 134 in intermediate nesting events, followed by SM&CDO (*n*=1,055) and BE (*n*=963). In total, 16 arribadas were recorded between 2016 and 2019, with durations ranging from 1 to 5 days. The interval between mass nesting events ranged between 16 and 75 days (Table 2).

**Table 2** Inter-arribada intervals in (days) at Corozalito. Values show the minimum and maximum number of days that could separate nesting events for individuals nesting between two arribadas, calculated from the first day of the earlier arribada to the last day of the subsequent one. Values followed by an asterisk (*) indicate inter-arribada intervals exceeding the longest IP documented for olive ridley turtles.

| Period between arribadas | 2016 | 2017 | 2018 | 2019 |
|---|---|---|---|---|
| 1st – 2nd | 44–46 | 39–47 | 16–20 | 28–33 |
| 2nd – 3rd | - | 19–25 | 70–75* | 25–30 |
| 3rd – 4th | - | 18–21 | 19–22 | 26–30 |
| 4th – 5th | - | 25–27 | - | 29–32 |

Over the study period, we recorded 555 previously tagged females at the three nesting locations, with multiple re-encounters resulting in a total of 650 nesting events involving previously tagged turtles (recaptures). The highest number of recaptures occurred at Corozalito (*n*=435), most of which were recorded during the arribadas (*n*=294, 67.6%), with fewer occurring during solitary nesting (*n*=128, 29.4%) and a small number as intermediate (*n*=13, 3.0%). Additionally, we recorded 215 recaptures at SM&CDO (*n*=137, 63.7%) and BE (*n*=78, 36.3%). Most recaptures corresponded to renesting events (*n*=493, 75.9%), while the remaining encounters were classified as remigrant events (*n*=157, 24.1%).

### Inter-beach movements

In total, we recorded inter-beach movements (intra and inter-seasonal) in ninety-nine olive ridleys (17.8%), whereas most individuals were re-sighted at the same nesting site where they had previously been recorded (*n*=456, 82.2%). Only one individual was observed switching nesting sites a second time, resulting in a total of 100 inter-beach movements. Most movements occurred within the same season (intra-seasonal; *n*=83, 83.0%), whereas fewer took place between seasons (inter-seasonal; *n*=17, 17.0%). These were not evenly distributed across nesting beaches: of the 100 recorded inter-beach movements, five were made from turtles tagged at Corozalito, accounting for just 1.7% of all individuals marked at the rookery that were later recaptured (*n*=300). In contrast, 95 movements were made by olive ridleys previously tagged at the neighboring beaches of BE and SM&CDO, representing 37.2% of all females marked at these two locations that were later recaptured (*n*=253). Notably, most of these movements occurred towards Corozalito (*n*=78, 82.1%) rather than between BE and SM&CDO (*n*=17, 17.9%).

Intra-seasonal movements from the neighboring solitary nesting beaches towards Corozalito were significantly more frequent during arribadas (*n*=43, 72.9%) than during solitary

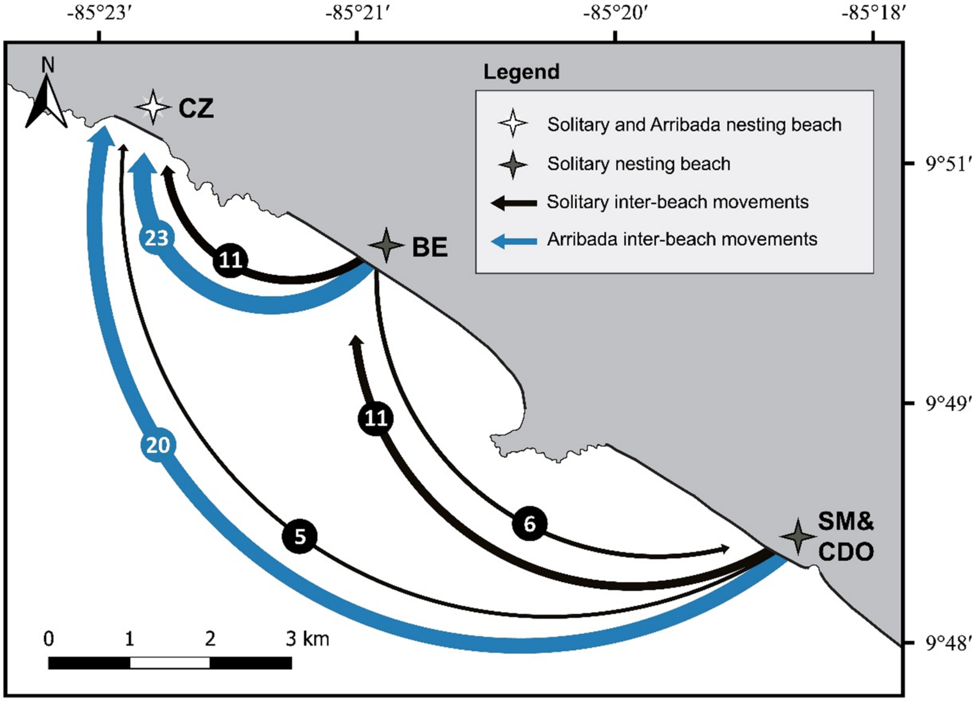

**Fig. 2** Intra-seasonal inter-beach movements of olive ridley turtles from the solitary nesting beaches of Bejuco (BE) and San Miguel and Costa de Oro (SM&CDO) toward Corozalito (CZ), as well as movements between the solitary beaches, during the study period. Movements from CZ ($n=5$) to the other beaches are not depicted. Arrow width is proportional to the number of movements towards the destination beach as a percentage of all movements from the origin beach. Arrow color indicates the behavior in which the female was recorded nesting at the final beach. Circles show the number of movements detected

**Table 3** Average inter-nesting period (IP) (±SD) in days for successive nesting events at olive ridley nesting beaches from 2016 to 2019, including the distinction between the four nesting behavior categories (AA, SA, AS, and SS)

| Beach and nesting category | 2016 | 2017 | 2018 | 2019 |
|---|---|---|---|---|
| CZ AA | 44.58±1.40 ($n=25$) | 38.13±12.24 ($n=24$) | 18.33±1.22 ($n=8$) | 29.93±1.31 ($n=2$) |
| CZ AS | 26.22±6.19 ($n=2$) | 21.67±6.46 ($n=3$) | NA | NA |
| CZ SA | 37.72±11.64 ($n=22$) | 39.41±11.03 ($n=33$) | 27.89±10.76 ($n=38$) | 25.83±6.82 ($n=15$) |
| CZ SS | 23.03±6.92 ($n=51$) | 23.06±7.71 ($n=63$) | 19.98±5.38 ($n=53$) | 20.67±6.29 ($n=28$) |

nesting ($n=16$, 27.1%) ($\chi^2_1 = 12.83$, $P=0.01$) (Fig. 2). Neither the origin beach ($\chi^2_2 = 0.04$, $P=0.95$) nor the nesting season ($\chi^2_3=0.3$, $P=0.95$) had a significant effect on movement frequency towards Corozalito (Table S1). In contrast, when considering only movements exhibited by females nesting in solitary within the same season, there was no significantly higher frequency of movements towards Corozalito ($n=16$, 49.5%) than between the exclusively solitary nesting beaches ($n=17$, 51.5%) ($\chi^2_1=0.03$, $P=0.86$) (Fig. 2). Similarly, neither the season ($\chi^2_1=0.82$, $P=0.85$) nor the origin beach ($\chi^2_3=0.27$, $P=0.61$) significantly influenced solitary nesting female movement frequency (Table S2). Finally, movements from Corozalito to the other sites were observed only in turtles initially tagged nesting in solitary, consisting of three movements towards BE and two towards SM&CDO. Notably, no turtle tagged in an arribada at Corozalito was later recorded at the other nesting sites.

## Inter-nesting period

IPs were calculated for 360 female olive ridleys that were recorded consecutively nesting within the same season. We were able to calculate two IPs for seven females across different seasons, totaling 367 registered IPs. A summary of the sample size and results by nesting behavior and location are shown in Table 3 and Figure S1. Because the sample size of AS IPs was very low and this category was represented only in two of the four seasons, it was excluded from subsequent statistical analyses Table 3. Although the sample size of AA IPs in 2019 was also small, these data were retained because the interval between consecutive arribadas that year was narrow and consistent, making the observed IPs representative of inter-arribada nesting intervals (Tables 2 and 3). All IP recorded between two arribada nesting events (AA) were obtained in consecutive arribadas.

Significant differences in IPs were observed among nesting behaviors across seasons at Corozalito (Kruskal–Wallis test: $\chi^2_{11} = 161.92$, $P<0.001$). Post hoc comparisons indicated that these differences were significant in IPs occurred in 2016, 2017 and 2018 seasons, whereas no differences in IP among nesting behaviors were detected in 2019. IPs between two arribada nesting events (AA) were significantly longer than those between two solitary nesting events (SS) in the 2016 and 2017 seasons, but not for 2018 or 2019. Additionally, IPs between a solitary nesting event and an arribada (SA) were significantly longer than those between two solitary nesting events (SS) in the 2016, 2017 and 2018 seasons. Finally, significant differences between AA and SA IP were obtained only for the 2018 season, with SA IPs being longer than AA IPs. Statistical details of these comparisons are provided in Supplementary Table 3.

## Discussion

### Inter-beach movements

Previous studies at mass nesting locations have reported olive ridleys nesting in arribadas to be less likely to change their future nesting location, than individuals nesting in solitary (Kalb 1999; Plotkin et al. 1995). Turtles nesting in solitary have been suggested to be responding to internal physiological stimuli that signal the commencement of their nesting event (Dornfeld et al. 2014; Kalb 1999). On the contrary, turtles nesting in arribadas, are suggested to be responding to external arribada-related cues that would help them synchronize (Barik et al. 2014; Bezy et al. 2020; Srikanthan et al. 2024), potentially overriding internal and physiological cues that govern timing in solitary nesting (Dornfeld et al. 2014; Kalb 1999). These external cues could have an attracting effect towards the mass nesting locations, making solitary nesters switch their previous nesting site and nesting behavior. Moreover, at other solitary nesting beaches located far from any mass-nesting rookery, strong nest site fidelity has been documented (Matos et al. 2012), suggesting that the drivers of spatial fidelity in olive ridleys could be affected by the proximity to a mass nesting location.

Our results suggest that arribadas indeed attract females from nearby nesting sites. We found inter-beach movements towards Corozalito occur more frequently during arribadas than during solitary nesting events. This may indicate that cues driving reproductive synchrony in olive ridleys attract females from nearby waters towards mass nesting locations (Bernardo and Plotkin 2007; Rojas-Cañizales et al. 2022). Nevertheless, our findings contrast with those of Dornfeld et al. (2014), who reported no change in solitary nesting activity at Playa Grande (Costa Rica) during arribadas at Nancite (40 km away) and Ostional (60 km away), indicating that turtles from Playa Grande did not shift to these mass nesting locations. One possible explanation is the greater distance between those nesting beaches compared with the nesting sites in our study, which are all located within 13 km of one another along the coast. This pattern suggests that the cues attracting turtles to arribadas may only be detectable over relatively short spatial ranges.

Studies of offshore olive ridley aggregations at mass nesting locations can provide further insight into the processes that may underlie inter-beach movement toward mass nesting locations. Bezy (2019) reported that offshore olive ridley aggregations at Ostional persisted year-round. Aggregation size fluctuated over time, likely as individuals joined and left the group, but these fluctuations were not associated with the timing of mass nesting events. Similarly, Kalb (1999) did not detect an increase in turtle density in offshore waters before or after the onset of arribadas. This appears inconsistent with the interpretation that stimuli preceding arribadas may attract females toward mass-nesting beaches. One possible explanation is that turtles nesting at the arribada location and at nearby nesting sites may already be aggregated in offshore waters within the relatively small spatial scale separating these beaches. At Rushikulya, these aggregations have been recorded extending more than 10 km along the coast (Rao et al. 2023). If turtles nesting at Corozalito and at nearby solitary nesting beaches share the same offshore aggregation, shifts of females toward the arribada rookery during mass-nesting events would not necessarily produce a detectable increase in the aggregation size. Accordingly, individuals from the shared offshore aggregation would typically emerge to nest at their preferred sites during solitary nesting but could shift toward the arribada rookery when mass-nesting events occur.

In line with this interpretation we found no difference in the frequency of exclusively solitary movements from BE or SM&CDO towards Corozalito compared to the movements between BE and SM&CDO. This suggests that females are not consistently attracted to nest at the rookery outside of arribadas. Evidence from other nesting sites indicates that movements toward Corozalito can also occur over much larger spatial scales. Rojas-Cañízales et al. (2022) documented inter-beach movements towards the rookery from other Costa Rican solitary nesting sites not included in this study, ranging from 8 km (Camaronal) to 222 km away (Osa Peninsula). These were recorded with a similar frequency in both arribada and solitary nesting. Movements from more distant locations may therefore reflect responses to cues associated with the formation of offshore aggregations rather than to the immediate onset of arribada nesting. In this context, turtles from distant rookeries could arrive in the region well before the start of the mass-nesting event to nest either in solitary or in arribada events. Nevertheless, compared with long-established sites such as Ostional and Nancite (Fonseca et al. 2009; Valverde et al. 1998), Corozalito represents a nascent arribada rookery. It is possible that the processes underlying offshore aggregations and the initiation of mass-nesting events at Corozalito may not yet be directly comparable to those documented at established mass nesting locations. Further research on the characteristics and dynamics of offshore olive ridley aggregations at Corozalito would help elucidate the mechanisms driving these movement patterns.

Inter-beach movements across the three nesting locations were strongly asymmetric. Almost no females that initially nested at Corozalito were subsequently recorded nesting at BE or SM&CDO. This pattern suggests higher apparent nest site fidelity at Corozalito relative to its neighboring nesting locations, regardless of nesting behavior. Our finding contrasts with Kalb (1999), who found stronger fidelity among females whose first nesting event of the season occurred during arribadas, suggesting that at Nancite, fidelity was more closely associated with nesting behavior than with nesting location. The mechanisms underlying the pattern observed at Corozalito remain unclear, but the pattern may suggest that once individuals recruit to the rookery, they remain associated with it across nesting events. Arribadas may decline as hatching success decreases due to excessive nest destruction, hypoxia, or microbial activity arising from very high-density nesting (Pritchard 2007). However, if arribadas are partially sustained or reinforced by immigration from surrounding areas, reduced local hatching success alone may be insufficient to explain their collapse (Rojas-Cañízales et al. 2022). Nevertheless, the extent to which inter-beach movements contribute to the maintenance or growth of arribadas remains unknown, as is whether these movements represent a primary driver of aggregation formation or a behavioral response to arribada-related social or environmental cues. Disentangling these mechanisms will be essential for understanding the long-term dynamics and resilience of mass-nesting systems in olive ridleys.

## Inter-nesting period

In olive ridleys, IP length can vary substantially depending upon the nesting behavior displayed (Bernardo and Plotkin 2007). Females participating in arribadas on their first nesting event of the season have been reported to exhibit longer IP than those that instead nest in solitary (Kalb 1999). While solitary nesting is generally thought to follow the internal reproductive cycle of individuals (Kalb 1999; Dornfeld et al. 2014), longer IPs in females nesting in arribadas could be attributed to delayed oviposition associated with reproductive synchrony (Bernardo and Plotkin 2007; Plotkin et al. 1997; Plot et al. 2012). However, IPs observed at Corozalito differ from those reported at Nancite by Kalb (1999), as we did not detect a consistent pattern in IP length among females nesting in arribadas across the four nesting seasons (Table 3).

During the 2016 and 2017 nesting seasons at Corozalito, IPs of females nesting in two arribada events (AA) were longer than those of females nesting in two solitary events (SS). In contrast, no significant differences between these categories were detected in the 2018 and 2019 seasons. In all AA IPs recorded, females nested in two consecutive arribadas; therefore, variation in the temporal spacing of successive arribadas directly influenced the AA IP observed within each season. Specifically, intervals between arribadas were considerably shorter in 2018, with the exception of one prolonged interval that exceeded the established maximum IP length reported for olive ridley turtles (66 days; Plotkin et al. 1995) (Tables 2 & 3). Such variation might be driven by differences in the environmental factors that influence the occurrence of arribadas (Barik et al. 2014; Bézy et al. 2020; Srikanthan et al. 2024). At Nancite, Kalb (1999) analyzed multiple nesting seasons without distinguishing among them and therefore did not capture seasonal variation. However, substantial interannual variation in arribada timing has also been documented at this rookery, with some mass nesting events being separated by more than 60 days and others occurring within the same month (Plotkin et al. 1995; Fonseca et al. 2009, 2023). Consequently, inconsistent patterns in AA IPs across seasons are likely to be common at rookeries where arribadas occur intermittently, as opposed to sites where mass-nesting events follow a more regular temporal pattern, such as Ostional (Valverde et al. 2012). Moreover, consecutive arribadas may be widely spaced in time, as observed in the 2018 nesting season at Corozalito, or limited to a single event per season, as reported for mass-nesting locations in India (Shanker et al. 2004). Under such conditions, females that have already nested during an arribada may be constrained to nest solitarily during their second nesting event, thereby adopting a mixed nesting strategy, further highlighting how irregular temporal patterns in arribada occurrence can shape nesting behavior.

At Corozalito, IPs of females nesting first in solitary and then in arribadas (SA) were longer than SS IPs in all seasons except 2019 (Table 3). Unlike SS IPs, SA IPs generally exhibited a greater variability. This variability may be associated with the timing of females joining offshore aggregations as well as the timing of both their previous solitary clutch and the subsequent arribada. Accordingly, females nesting their second clutch in solitary (AS and SS) would be expected to have shorter and less variable inter-nesting periods (IPs) as they would not delay oviposition in order to synchronize (Plot et al. 2012). However, we detected no significant differences between SA and SS IPs for the 2019 nesting season. The factors underlying this pattern remain unclear, and additional data would be required to determine whether it reflects short-term variability or a biologically meaningful shift. In addition, sample size for AS IPs was insufficient to allow statistical inferences. At Nancite, Kalb (1999) reported shorter SA IPs (17.1 ± 2.1 days, $n = 5$) than AS IPs (40.6 ± 2.9 days, $n = 7$). Although these results appear to contrast with our proposed explanation of the influence of synchronic nesting on IP length, the small sample sizes and lack of seasonal resolution in Kalb's study limit direct comparisons. Nevertheless, the factors determining whether individuals adopt mixed nesting strategies (SA or AS) remain poorly understood and may also include physiological or individual-level constraints related to reproductive timing.

Finally, the SS IPs obtained did not differ among seasons and were comparable to those reported for other rookeries; including Punta Banco (19.95 ± 4.04 days, $n = 240$; Viejobueno and Arauz 2015), Nancite (20.7 ± 1.4 days, $N = 10$; Kalb 1999), Sergipe (22.35 ± 7.01 days, $N = 143$; Matos et al. 2012) São Tomé and Principe (22.93 ± 4.39, $N = 415$; Hancok et al. 2019) and Playa Grande (24.5 ± 7.1 days, $N = 33$; Dornfeld et al. 2014) (Table 3). These short and consistent IPS align with solitary nesting following a predictable physiological pattern across several locations (Dornfeld et al. 2014; Kalb 1999). In contrast, IPs recorded for females nesting in arribadas reflect the timing and frequency of mass nesting events at the rookery, and for rookeries with irregular arribada patterns such as Corozalito, a marked interanual variation can be expected. A limitation of this study is that environmental factors known to influence IPs, such as sea surface temperature (Fuentes-Tejada et al. 2025), were not explicitly considered, which may explain some of the observed variations. Future studies at Corozalito and other arribada rookeries should investigate how nesting synchrony, environmental, and physiological factors interact to shape inter-nesting periods, providing a deeper understanding of the flexibility and constraints of sea turtle reproductive strategies.

## Metal tagging studies limitations

During the study period, we observed a difference in recaptures between renesting ($n = 495$, 75.9%) and remigrant events ($n = 157$, 24.1%). Recapture rates can be influenced by factors such as tag loss, mortality or movements towards other nesting beaches not surveyed in this study (Cornelius and Robinson 1986; Hancock et al. 2019; Hays et al. 2003). Furthermore, tag recapture may also be lower during arribadas than in solitary events at Corozalito due to the difficulty of detecting tagged turtles among the large number of nesting females that participate in the event (Cornelius & Robinson-Clark 1986, Rojas-Cañizales et al. 2022). Finally, at Corozalito, tagging saturation was feasible for solitary nesting but not for arribada events, due to the sheer numbers of females present during mass nesting events. Together, these factors represent a limitation of our study and may have contributed to the uneven sample sizes across behavioral categories (AS: $n = 5$; SA: $n = 108$) and between seasons within a category (AA 2016: $n = 25$; AA 2019: $n = 2$) at Corozalito (Table 3).

## Conclusion

This study sheds lights on how nesting behaviors can influence the spatial and temporal nesting dynamics of olive ridleys. Our results provide some of the first empirical evidence that arribadas may attract nearby nesting females at short distances, prompting beach exchange. We have also observed higher nest site fidelity at Corozalito, regardless of the nesting behavior displayed, compared to its neighboring nesting beaches. Although further research is needed, this pattern provides insight into the initiation and evolution of nascent arribada sites like Corozalito. Expanding this approach to more distant nesting sites could help determine the spatial reach of movements associated with arribadas, improving our understanding of the processes involved in the formation and persistence of mass-nesting locations. Our results also show that IP length can vary with nesting behavior, but this pattern is not consistent across nesting seasons. Instead, IP variability appears to be closely linked to the frequency and timing of arribadas, as well as to the previous individual nesting history earlier in the season. As a result, females nesting in an arribada on their first event of the season do not always have a longer IP than those that nested in solitary as previously thought. Finally, the documented connectivity among neighboring nesting beaches highlights that conservation efforts at arribada rookeries should not be restricted to the focal mass-nesting site alone, but should instead adopt a broader, landscape-scale perspective that accounts for inter-beach movements. Despite its growing importance as an arribada site, Corozalito and its surrounding waters remains unprotected by the Costa Rican government, underscoring the urgent need for formal protection measures that reflect its ecological significance and regional connectivity.

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**Data availability** The authors declare the availability of the data upon reasonable request.

**Code availability** Data supporting the findings of this study are included in the supplementary material.

## Declarations

**Conflict of interests** The authors declare that they have no personal or financial conflicts of interest that could affect this work.

**Ethics approval** This study has been approved by MINAE, SINAC and ACT of Costa Rica, research permits [ACT-OR-DR-112-16; ACT-OR-DR-109-17; ACTOR-DR-006-19 and ACT-OR-DR-084-19].

**Consent to participate** The authors declare that they participated in this research.

**Consent for publication** The authors agree and give their consent for the publication of this study.

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