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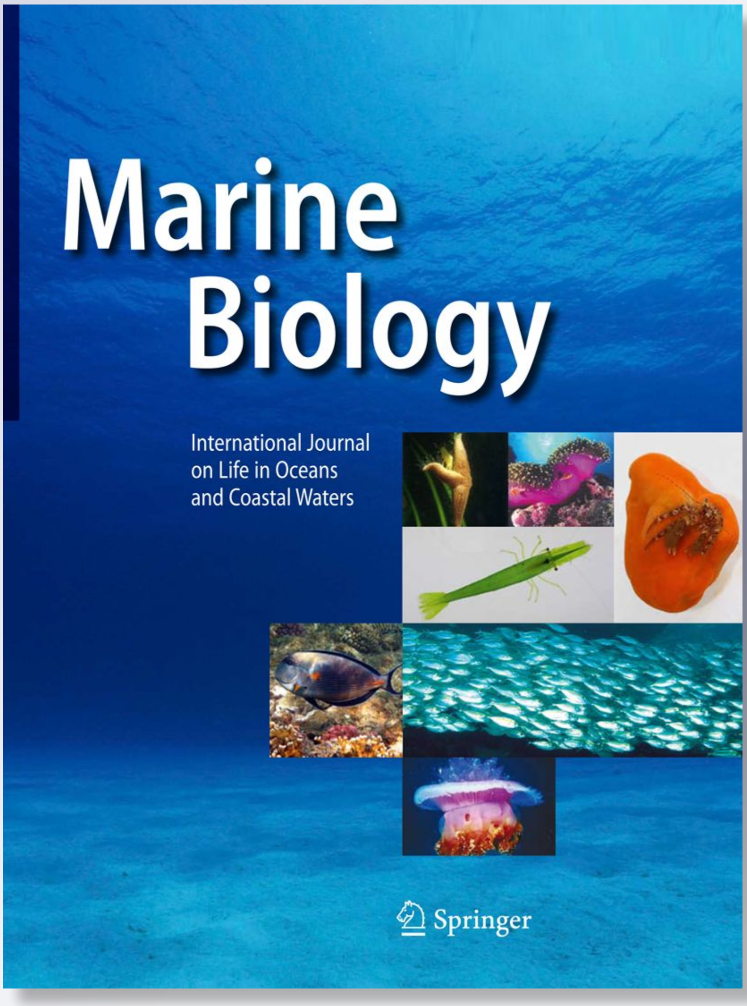

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ORIGINAL PAPER

Strong site fidelity and longer internesting interval for solitary nesting olive ridley sea turtles in Brazil

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Abstract Olive ridley sea turtles display two different types of nesting behavior: in *arribada* (synchronous mass nesting) or solitarily. Contrarily to *arribadas*, little has been published about solitary nesters. This study aimed to expand the knowledge on internesting interval and site fidelity of solitary nesting olive ridleys and to test a possible development of *arribada* nesting behavior. Data were collected in Sergipe (Brazil) over 125 km of beach from 10°30′S/36°23′W to 11°26′S/37°19′W, between nesting seasons 2004/2005 and 2006/2007. From 962 tagged females, 173 were seen renesting. The average internesting interval found was longer (22.35 ± 7.01 days) than previously described, which might relate to lower water temperatures during the internesting period. Olive ridleys at Sergipe showed high nesting site fidelity, with consecutive nesting events occurring in close proximity, non-randomly and dependently of previous events. Most of the consecutive nests were separated by 4.06–5.59 km. Development of *arribada* nesting behavior was not confirmed.

Introduction

Sea turtles are widely known for their ability to return to their birth region to nest. This ability (philopatry) differs from a finer and consecutive homing to beach, named site fidelity. Nesting site fidelity is detectable between nesting seasons when turtles migrate from foraging to reproduction areas, as well as within nesting seasons (Miller 1997). Female turtles lay several clutches each nesting season and tend to renest in close proximity (Miller 1997). Nesting site fidelity creates spatial and temporal patterns on sea turtles' reproduction ecology that is usually distinct on either specific or populational levels. Reproduction periodicity within a season, called internesting interval, is the number of days between consecutive nesting events (Alvarado and Murphy 1999).

In populations of olive ridley sea turtles, *Lepidochelys olivacea*, two distinct types of reproductive behavior may occur. Females can either emerge to the beach in large synchronized *arribadas* (the Spanish expression for mass nesting event), or they will emerge solitarily, meaning alone or in a small group but without synchrony (Kalb 1999). Major *arribada* nesting occurs at very few remaining rookeries such as Rushikulya (India), Playa Escobilla (Mexico), and Ostional (Costa Rica), while solitary nesting

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happens throughout the species' range (Bernardo and Plotkin 2007).

Whereas *arribadas* have been relatively well documented, information on the dynamics of solitary nesting is limited. A general comparison indicates that *arribada* nesters have a four-week internesting interval and high-level site fidelity, while solitary nesters show a much shorter two-week internesting interval and low-level site fidelity (Kalb 1999; Bernardo and Plotkin 2007). The few studies on solitary nesters have been mainly conducted in the eastern Pacific. Described internesting interval varies from 15 to 17 days (sample size: $N = 22$) in Punta Ratón, Honduras (Minarik 1985); from 16 to 20 days ($N = 31$) in Punta Banco, Costa Rica (Naranjo and Arauz 2004); and averages 20.7 days ($N = 10$) for exclusive solitary nesters within the *arribada* rookery of Nancite, Costa Rica (Kalb 1999). More recently, non-*arribada* olive ridley's internesting interval was reported as 16.7 days ($N = 3$) for the North Australian population by Whiting et al. (2007) and as 17.5 days ($N = 13$) for the Central African Atlantic population by Maxwell et al. (2011).

In Pirambu (Sergipe, Brazil), regular night patrols have been conducted since the beginning of Projeto TAMAR—ICMBio, the Brazilian Program for Sea Turtle Conservation. Nonetheless, it was only during the 2004/2005 nesting season that a systematic internesting registry was initiated in this area. Preliminary data on internesting interval (Castilhos and Tiwari 2006; Matos et al. 2008) indicated longer intervals than those expected based on the literature; thus, encouraging further research. Sergipe is the key choice for an intensive study. Firstly because of its strictly solitary population, where no *arribada* effects may interfere. Secondly, olive ridleys' solitary behavior has never been documented for any Western Atlantic population; though small *arribadas* have been studied during the late 60s at Eilanti, Suriname (Pritchard 1969a, b; Schultz 1975) and recently at Cayenne, French Guiana (Plot et al. 2011). Moreover, the Brazilian nesting population may presently be the largest within the West Atlantic region and with a rapid population growth (Marcovaldi 2001; Godfrey and Chevalier 2004; Silva et al. 2007). This upward trend was suggested to result from increased recruitment since both average curved carapace length (CCL) and average clutch size seem to be decreasing. Both aspects are believed to be typical of younger, smaller nesting females (Silva et al. 2007).

While comparing solitary and *arribada* nesting behavior, Kalb (1999) suggested solitary nesters to be neophytes nesting in cycles determined physiologically. Their still undeveloped capacity of retaining eggs and wait for an *arribada* explained the shorter internesting intervals observed (Kalb 1999). Shorter reproductive seasons with a lower energy loss should enable these females for greater displacements during the internesting period (Kalb 1999). Therefore, a gradient should be seen toward longer internesting intervals and stronger fidelity as females grow older. If a solitary rookery such as Sergipe's would mature until develops *arribada* nesting, then these patterns should be detectable.

The current study evaluates the internesting interval and site fidelity of olive ridleys in the solitary rookeries of Sergipe. Additionally, the suggested relationship (Kalb 1999) between female maturation level and duration of internesting interval was tested, as well as between this and the degree of nesting site fidelity.

Methods

Study site

This study was conducted on the State of Sergipe (Brazil), on Projeto TAMAR research unit, where nesting activity is monitored at three field stations: Ponta dos Mangues (36 km), Pirambu (53 km) and Abaís (36 km), covering 125 km of beach between latitudes 10°30′S and 11°25′S. We excluded the central area of Sergipe's coast around the state capital Aracaju from monitoring due to very low nesting densities likely caused by anthropogenic pressure. This area separates geographically Abaís on the south from Pirambu and Ponta do Mangues up north. The three sampled areas were divided into marked sections; each section was identified by a specific beach name (Fig. 1). With the exception of Barra dos Coqueiros beach, all other beaches in Pirambu field station were marked with stakes at 1-km intervals. Sergipe's coastline contains high-energy beaches with an open, rock-free offshore approach. Four major rivers discharge along the coastline causing some turbidity (Silva et al. 2007).

Data collection

We collected and recorded the data applying the general methodology of Projeto TAMAR (Marcovaldi and Laurent 1996; Marcovaldi and Marcovaldi 1999; Silva et al. 2007). We patrolled the beaches every night during the nesting season, for the female tagging program. Depending on the tides, one or two patrols were performed each night, with two or more observers. Surveillance was favored where higher nesting records were historically observed. We measured (according to Bolten 1999) and tagged (according to Balazs 1999) every nesting turtle encountered using Inconel flipper tags (size: 2.5 cm; Style 681, National Band and Tag Company of Newport, Kentucky, USA), placed with a standard applicator, next to the first large proximal scale of each front flipper. Tagging allowed further recognition of the females. For each nesting event, we recorded

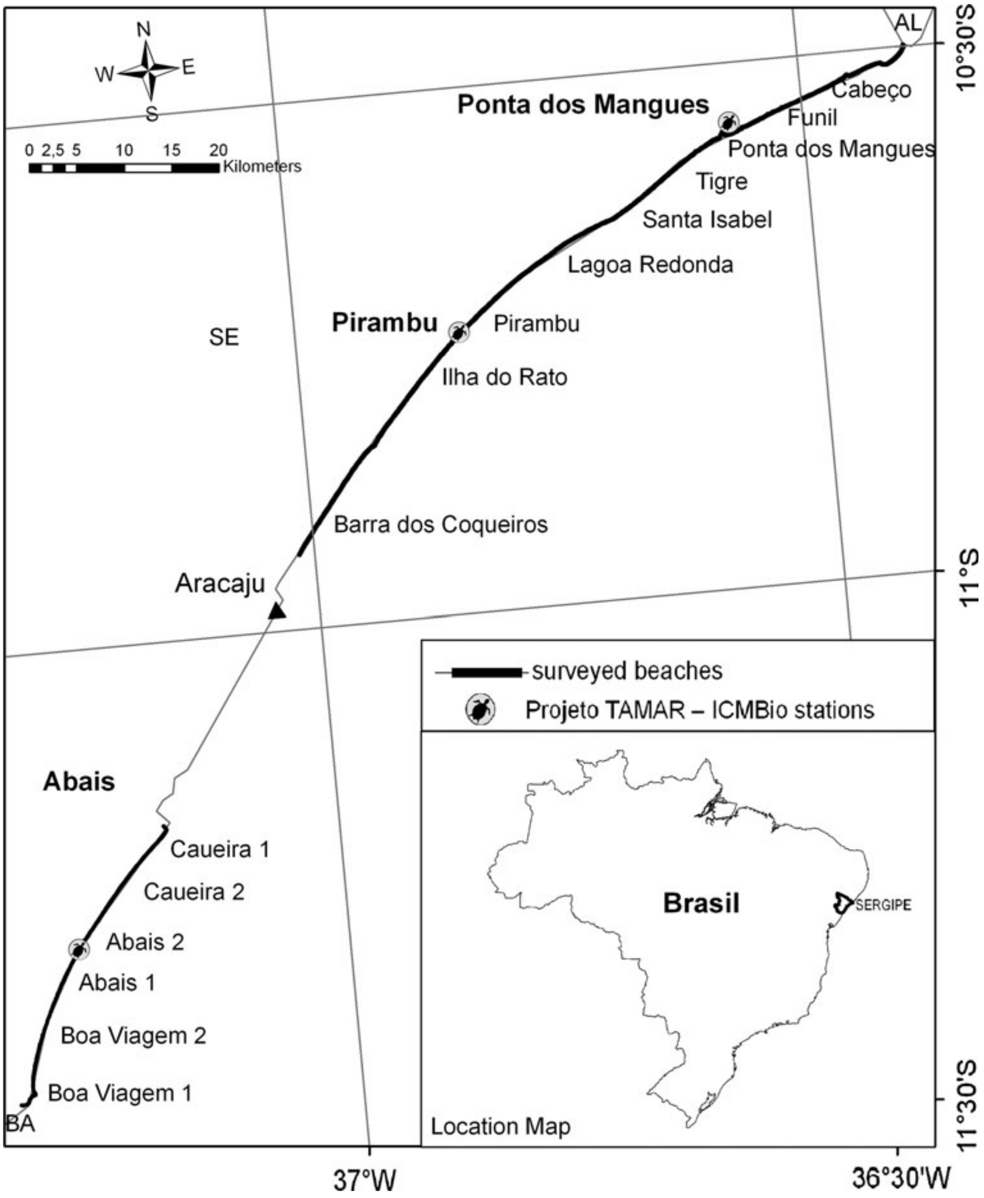

Fig. 1 Map of Sergipe (SE), including names of surveyed beaches of the three Tamar field stations: Abais, Pirambu and Ponta dos Mangues. The state is limited by Alagoas (AL) in the North and Bahia (BA) in the South

date, hour and location, as well as successful status of the event.

The nesting season for olive ridleys in Brazil extends from September to March. We performed regular fieldwork each year, from September, 15th to March, 15th. Outside the regular monitoring period, information on nesting occurrences was obtained only opportunistically, representing no more than 1–2% of the total annual (Silva et al. 2007). We collected the data between July, 1st 2004 and April, 10th 2007, thus considering three consecutive nesting seasons: 2004/2005, 2005/2006 and 2006/2007.

Data analysis

We calculated a new renesting event whenever we recaptured a female within the same nesting season. When females were seen renesting more than once, all renesting events were considered. We classified renesting events into two categories: renesting attempts (aborted nesting followed by successful nesting) and internesting intervals. The internesting interval was calculated using two distinct criteria: (a) intervals between consecutive successful nests; and (b) intervals between a successful nest and the next attempt, successful or not. Aiming to validate comparisons with previous published literature on internesting intervals, we statistically compared results from the two criteria employing the Mann–Whitney U Test (Zar 1999). We found no significant difference neither between the internesting intervals ($U = 9287.5$, $N_1 = 132$, $N_2 = 143$, $P = 0.818$) nor between the distances calculated for each criterion ($U = 7312.5$, $N_1 = 117$, $N_2 = 126$, $P = 0.914$), thus allowing the referred comparisons. All results presented here correspond to the second criterion described above. We discarded intervals below 6 days from the analysis because sea turtles are physiologically unable of laying two different clutches in less than 6 days (Miller 1997). Likewise, we considered intervals longer than 66 days to be multiple laying intervals, since that is the largest internesting interval ever observed (Plotkin 1994). These were also removed from the analysis. Intervals between 6 and 66 days were not split into multiple intervals (as usually done for other sea turtles) because olive ridleys are known to be capable of prolonged egg retention (Plotkin 1994). Therefore, despite being within the range of other published results, the internesting interval may be overestimated, once some renesting events might have been lost.

To evaluate nesting site fidelity, we compared distances performed between renesting attempts with those performed in internesting intervals. Statistical comparison was done using Mann–Whitney *U* Test (Zar 1999). We only took into account occurrences within the 34 km of Pirambu's coastline marked with kilometer stakes (Rato, Pirambu, Lagoa Redonda and Santa Isabel beaches). Location of events was considered to be the same as the kilometer marked on the beach. This way, we reduced associated errors of events' location to less than 1 km.

We further investigated fidelity through randomness of consecutive nesting events. Using the same data set, we assumed that in a completely random situation, the various distances performed between events would have approximately the same frequency in the population. Therefore, if we plotted all distances and then split that distribution in the middle, we would expect to have the same accumulated frequency on the two groups of equal halves (e.g. if 20 km is the maximum distance observed, then there should be as many occurrences from 0 to 10 km as from 10 to 20 km). We applied χ^2 tests to evaluate the departure of observed data from expected values (Zar 1999), considering two, three and four groups of equal distances.

We tested independence between consecutive events of each female by creating contingency tables with location of first and second events and using a G^2 test of independence on the log-likelihood ratio (Nordmoe et al. 2004). Due to test requirements, we regrouped nesting occurrences in beaches thus avoiding low or null frequencies. Only Pirambu, Lagoa Redonda, Santa Isabel, Tigre and Ponta dos Mangues beaches were considered for this analysis.

Additionally, we performed linear regressions to test Kalb's (1999) suggestions for relationships between maturation of females, duration of internesting interval and displacement during that period. We used female size (CCL) to approximate female age (Snover et al. 2007) and distance between consecutive nests to determine internesting displacement.

In all statistical approaches, we set the cut-off for significance at 0.05.

Results

Internesting interval

During the 3-season survey, we recorded 1,343 encounters with nesting females on the three field stations, mainly occurring at Pirambu field station. We tagged 962 females and observed 173 renests within the same nesting season, enabling a total computation of 202 renesting events.

We found an average internesting interval (mean ± standard deviation) of 22.35 ± 7.01 days ($N = 143$). Following a successful nesting, the majority (mean ± confidence intervals) of females renested within a period of 21.2–23.5 days (Fig. 2). However, after an aborted nesting, many turtles attempted to renest within the first 6 days. The average interval for these renesting attempts was 9.25 ± 10.12 days ($N = 57$).

Site fidelity

We investigated nest site fidelity at Pirambu, Lagoa Redonda and Santa Isabel beaches analyzing internesting intervals and renesting attempts separately. Renesting attempts showed no particular distribution pattern (Fig. 3). In contrast, we found a pattern within internesting intervals' events: females renesting closer to a previous nest location. Distances registered for internesting intervals were significantly smaller than those found for renesting attempts ($U = 2{,}345.5$, $N_1 = 47$, $N_2 = 126$, $P = 0.035$). The average distance between internesting events was 4.83 ± 4.37 km ($N = 126$). The majority (mean ± confidence intervals) of internesting distances varied between 4.06 and 5.59 km.

Additionally, there was no significant relationship neither between the size of the female (CCL) (Fig. 4) and the internesting interval ($r^2 = -0.008$, $N = 132$, $P = 0.909$) nor between the internesting interval and the distance between consecutive nests ($r^2 = -0.008$, $N = 116$, $P = 0.816$).

When split into two groups, location of nesting events proved to be not random ($\chi^2_1 = 67.175$, $P < 0.0001$) as the second event tended to be located close to the first. Observed internesting events at close proximity have higher frequencies than expected. On the other hand, observed internesting events further apart have lower frequencies than expected (Fig. 5). Refinement of the analysis with three or four groups reinforces the result obtained with the analysis of two groups. The independency test for consecutive nesting events showed the existence of nesting site fidelity, as the location of the second nesting event is dependent on the location of the first ($G^2_{16} = 34.093$, $P < 0.01$).

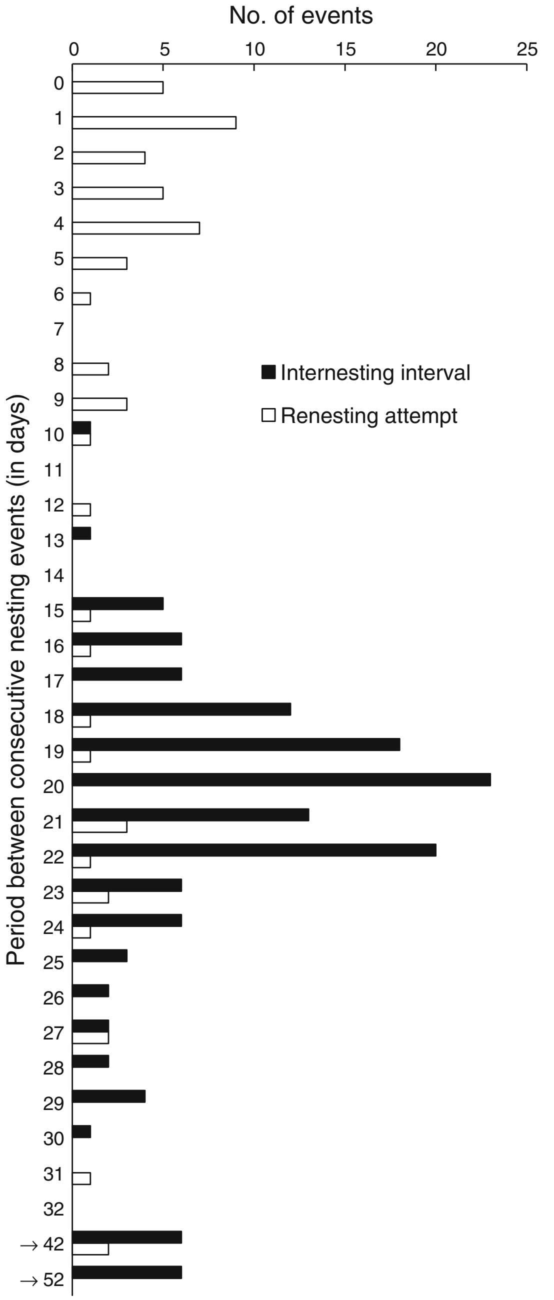

Fig. 2 Period (in days) between consecutive nesting events of olive ridleys found at Sergipe: internesting intervals, that is, the interval between a successful nest and the next attempt, successful or not (in *black*); and renesting attempts, that is, an aborted nesting followed by successful nesting (in *white*)

Discussion

Internesting interval

We found ridleys' population in Sergipe to have longer internesting intervals than all solitary nesting populations described in the East Pacific (Minarik 1985; Kalb 1999; Naranjo and Arauz 2004), Australia (Whiting et al. 2007) and Central African Atlantic (Maxwell et al. 2011). However, since renesting events could have been lost and longer intervals were not split into possibly multiple intervals, some overestimation might be present (see "Methods" section).

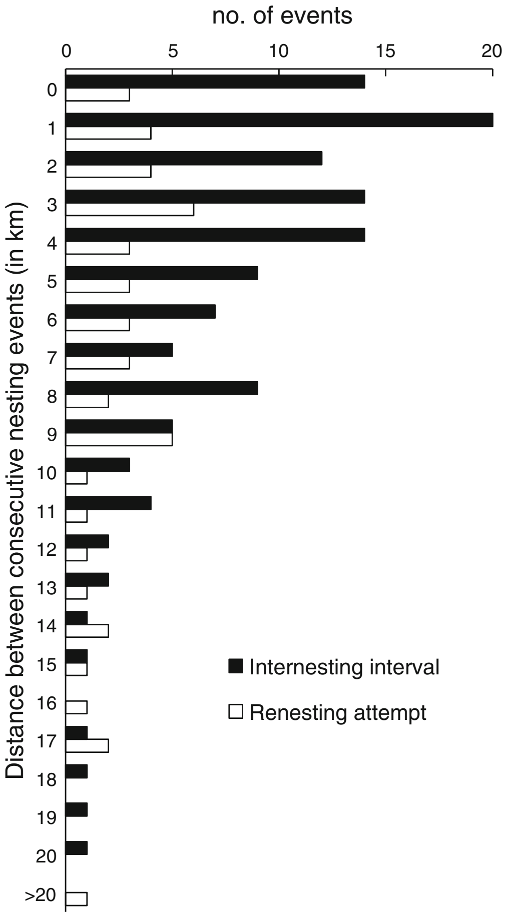

Fig. 3 Distance (in km) between consecutive nesting events of olive ridleys found at Pirambu: internesting intervals, that is, the interval between a successful nest and the next attempt, successful or not (in *black*); and renesting attempts, that is, an aborted nesting followed by successful nesting (in *white*)

Longer internesting intervals might be related to the existence of a cooler sea water temperature decelerating the rate of pre-ovipositional development of eggs during internesting, as it has been described for loggerheads and green turtles (Sato et al. 1998; Webster and Cook 2001). Since sea turtles are essentially ectothermic animals, their metabolic rate generally increases with sea water temperature (Hays et al. 2002). Smaller loggerhead and green turtles, with lower body mass, tend to have their body temperature closer to the environment, possibly because of lower accumulation of metabolically produced heat (Sato et al. 1995). Thus, water temperature influences general metabolic rate and consequently nesting activities (Sato et al. 1998; Hays et al. 2002; Mazaris et al. 2004). This

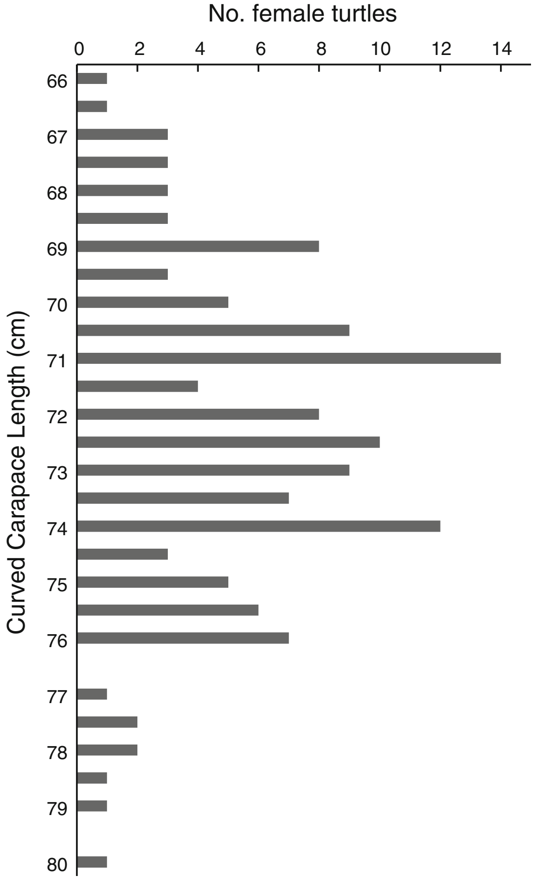

Fig. 4 Size (in cm) of female olive ridley turtles found at Sergipe, measured as curved carapace length (CCL)

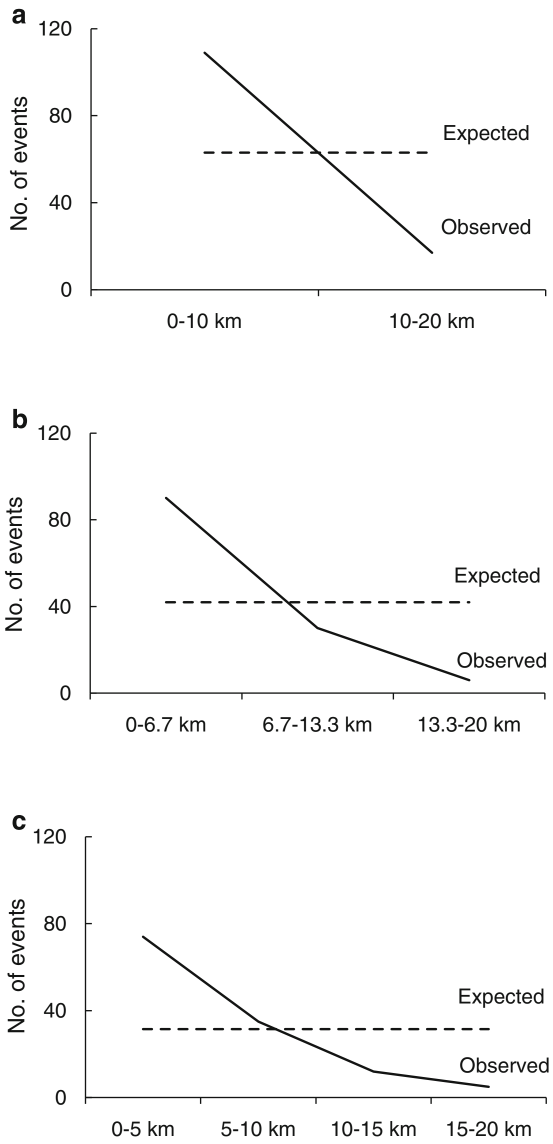

Fig. 5 Graphical display of the randomness analysis of consecutive nesting events using (**a**) two, (**b**) three and (**c**) four groups of equal distances, respectively

tendency also seems to occur among sea turtle species. With the exception of the flatback turtle (*Natator depressus*), smaller species tend to have longer internesting periods (Davenport 1997; Miller 1997). As one of the smaller species, olive ridleys' body temperature and metabolism should be quite influenced by water temperature. Cooler areas are, therefore, expected to decrease their metabolism and, consequently, extend internesting intervals (Sato et al. 1998). Unexpectedly, Hamel et al. (2008) found no apparent relationship between internesting interval and water temperature on Australian olive ridleys; nonetheless, sample size was small ($N = 2$). Further studies should be conducted in order to test this hypothesis.

The observed longer internesting intervals at Sergipe could also be related to phylogenetic differences of this population. Previous studies suggested that after the evolutionary divergence of the two *Lepidochelys* species (after Panama's isthmus closed), olive ridleys expanded their geographic distribution from the Indio-West Pacific region to the East Pacific and, more recently, to the Atlantic Ocean (Pritchard 1969a, b; Hughes 1972; Bowen et al. 1998). If the Atlantic coast was the last to be colonized, then genetic divergence could have occurred during the geographic expansion, justifying differences in reproductive patterns between different populations. Distinct genetic compositions have been found in Atlantic olive ridley populations (Bowen et al. 1998). They exhibit exclusive mitochondrial DNA alleles F and E; however, relationships between genotype and phenotype have not yet been made.

With longer internesting intervals, longer residence times are expected for female olive ridleys at Sergipe (Miller 1997; Hays et al. 2002), increasing the females' susceptibility to human activities at sea. The existence of a wandering behavior during the internesting period will amplify this susceptibility (Whiting et al. 2007). Recent satellite-tracking studies from Sergipe point out to wide internesting areas (most of Sergipe's coastline) that overlap with fishing areas (Silva et al. 2011). Sergipe is an important area for shrimp trawling and negative interactions with turtles occur in the region (Marcovaldi et al. 2006; Silva et al. 2007). Conservation measures are needed, including: law enforcement of fishing exclusion zones (Thomé et al. 2003); extension of the summer fishing closure and development of a suitable management plan for the trawling fleet (Silva et al. 2010).

Site fidelity

Carr and Carr (1972) have proposed that a probable advantage of the nesting site fidelity was the possibility of retaining favorable nesting places. Hence, a female would produce more offspring, increasing its fitness (Kamel and Mrosovsky 2005).

Olive ridleys' nesting in Brazil is concentrated around Sergipe (and mainly in Pirambu) although an extensive shore with hundreds of kilometers of open-sandy, rock-free coastline also seems suitable. Consecutive nesting events occurred in close proximity, non-randomly and depended on previous events. Additionally, the smaller distance performed between internesting intervals (when compared to renesting attempts) might indicate the females' capacity of nesting choice based on the conjecture that females aborting a nesting are deciding to search for a more suitable nesting place.

Previous publications have characterized olive ridleys nesting site fidelity based on its ability to return to a specific beach (Kalb 1999; Whiting et al. 2007) or expressed in broad space intervals (Maxwell et al. 2011). Here, we determine an average distance between consecutive nests perform by the females. Our findings are within those reported for example for loggerhead turtles of Florida (USA) and Natal (South Africa) that presented average internesting distances mostly between 3 and 6.9 km (Schroeder et al. 2003). Generally, sea turtles are said to renest in close proximity (up to 5 km) of previous nesting (Miller 1997). Overall, with an average distance between internesting events of 4.83 km, the Brazilian olive ridleys can be considered to present strong site fidelity.

Testing Kalb's suggestion (1999), we found no relationship between maturation level of females and internesting intervals (CCL use as an estimation of age). It is possible that no relationship exists between age and duration of internesting period. However, if no ecological triggers to set an *arribada* are present at Sergipe, then older turtles would not need to retain their eggs. This way, they would present similar internesting intervals as neophytes, masking that relationship. We also found no statistical relationship between internesting intervals and distances between consecutive nesting events in Sergipe. Nevertheless, recent studies with satellite tagged ridleys from Sergipe seem to show internesting displacement to be greater than the distance between consecutive nesting events (Silva et al. 2011). In Australia, two female olive ridleys travelled 125 and 200 km during internesting, returning to nest within 3 and 10 km away from original nesting site, respectively (Hamel et al. 2008). Both internesting displacement and age need further evaluation, if their relationship with internesting intervals is to be precisely verified.

Conclusions

This study is the first to evaluate internesting intervals and site fidelity of solitary nesting olive ridleys on the West Atlantic. Sergipe holds a growing nesting population under active conservation measures for 30 years (Silva et al. 2007) with generally low human presence that should promote relatively natural conditions for the rookery.

Arribada nesting areas gather large female populations, but their existence depends on small areas, very sensitive to human disturbance and stochastic events (Plotkin and Bernardo 2008). The more cosmopolitan solitary nesters may outnumber *arribada* nesters worldwide (Bernardo and Plotkin 2007) and show less sensitivity (Godfrey and Chevalier 2004). Although conservation measures taken at *arribada* areas are important, other efforts should be taken in consideration at solitary nesting grounds. The development of further studies and conservation actions on olive ridley solitary nesting grounds might be crucial for the species preservation.

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Ethical Standards Metal tagging of flippers used in this study is a widespread and frequent approach used in mark–recapture programs designed for long-term monitoring of individual sea turtles (Chaloupka and Musick 1997). So far, we have never noticed any adverse effect on the turtle's behavior and well-being throughout our long-term monitoring program. All procedures were approved by ICMBio—Instituto Chico Mendes de Conservação da Biodiversidade (national institute for biodiversity conservation).

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